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Seasonal Movements, Habitat Utilization, and Comparative Scale Morphology of White Marlin (Kajikia albida) and Roundscale Spearfish (Tetrapturus georgii)

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Seasonal movements, habitat utilization, and comparative scale morphology of white marlin (*Kajikia albida*) and roundscale spearfish (*Tetrapturus georgii*)

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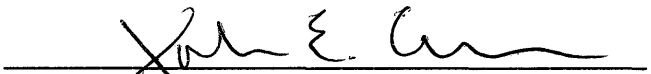

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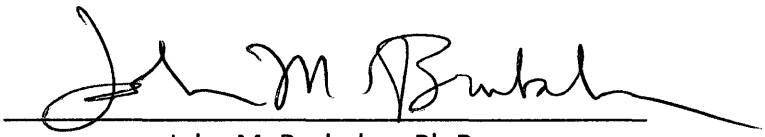

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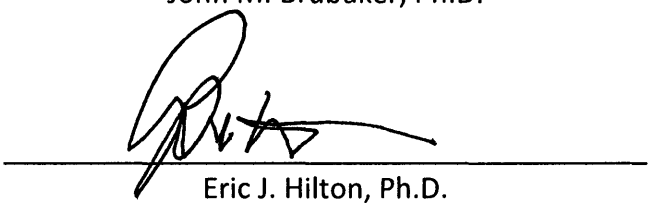

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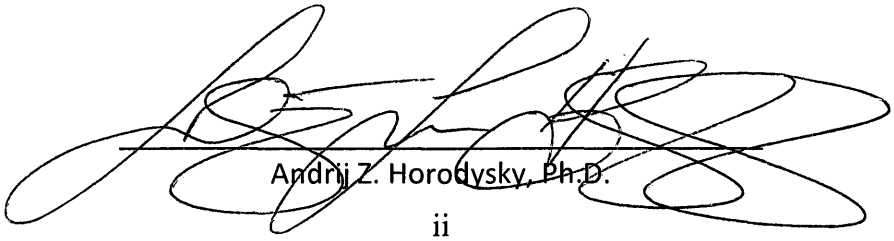

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DEDICATION

To my mother, Linda Malee Loose (1947-2011), who wholeheartedly supported me in every adventure I have ever chosen, from traveling alone in remote corners of the globe to embarking on the journey through graduate school. Although my mom was very proud to see me start at VIMS, she was unable to see the completion of my journey here, and I dedicate this thesis to her memory.

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ABSTRACT

Recent studies have demonstrated that the morphologically similar white marlin (*Kajikia albida*) and roundscale spearfish (*Tetrapturus georgii*) co-occur in the western North Atlantic, including the U.S. Mid-Atlantic Bight. Differences in scale morphology have been proposed as one morphological character to discriminate these species, but a thorough analysis of scale morphology is lacking. Because the validity of the roundscale spearfish was not established until 2006, much of the biological information previously collected for "white marlin" may include data for both white marlin and roundscale spearfish. The objectives of this study were to obtain a better understanding of the movements and habitat utilization of positively identified white marlin that inhabit the U.S. Mid-Atlantic Bight during summer months, and to describe the morphological variation of white marlin and roundscale spearfish scales.

Eleven long-term (6 or 12 month) pop-up satellite archival tags were placed on white marlin that were caught and released in the U.S. recreational fishery. Nine tags reported information on temperature, pressure (depth), and light levels for light-based geolocation for periods of 8 days to 12 months. Most fish moved out of the Mid-Atlantic Bight in September, and overwintered in areas ranging from east of the Gulf Stream off the Carolinas to the Caribbean, and as far south as northern Brazil. Of the seven fish that retained tags for more than 40 days, five spent time in known spawning grounds in waters of the Dominican Republic leading up to the spring spawning season. These data demonstrate a large degree of connectivity among white marlin in the western North Atlantic. As noted in previous studies, individuals spent a large proportion of their time in the surface waters (0-10 m; 75% across all white marlin pooled), the vast majority of their time in the top 100 m of the water column (97%), and within eight degrees of sea surface temperature (98%), although definite shifts in habitat utilization were evident as fish departed coastal offshore waters of the Mid-Atlantic Bight. Diel habitat utilization varied greatly, with white marlin spending 81% of total nighttime in the surface waters (0-10 m), and only 26% of total daytime in surface waters.

Past studies have characterized the scales of white marlin and roundscale spearfish as being morphologically distinct, but little effort has been made to describe variation within an individual, among individuals, or between species. To better understand morphological variation of scales and squamation patterns of distinct body regions of these two species, individual scales were collected from 11 specific anatomical regions, and scale patches were collected from 3 specific regions of each white marlin and roundscale spearfish brought into marlin tournament weigh stations in the Mid-Atlantic Bight during 2012 and 2013. Scales were measured and described, and scale patches were cleared and stained to examine the level of imbrication of the scales, as well as the overall squamation patterns. In addition to the scales, denticular plates, ossified formations occurring on the surface layer of the dermis, were measured and described. Although considerable

morphological variation was observed among scales from different anatomical regions of individuals of both species, white marlin scales generally have pointed anterior ends, fewer posterior points, and are more heavily imbricated than those of roundscale spearfish, which are frequently rounded anteriorly, but often have many posterior points and are farther separated within the skin. Over all areas and individuals, roundscale spearfish scales were significantly wider and had a lower length-to-width aspect ratio than those of white marlin. Detailed scale descriptions allow for a more accurate characterization of the variation within and differences between these two species, and could potentially be a valuable tool for investigating istiophorid systematics.

SEASONAL MOVEMENTS, HABITAT UTILIZATION, AND COMPARATIVE SCALE MORPHOLOGY OF WHITE MARLIN (*Kajikia albida*) AND ROUNDSCALE SPEARFISH (*Tetrapturus georgii*)

CHAPTER 1

GENERAL INTRODUCTION

INTRODUCTION

The billfishes (family Istiophoridae) include the marlins, sailfish, and spearfishes. Within the Atlantic Ocean there are six species of istiophorid billfishes: blue marlin (*Makaira nigricans*), white marlin (*Kajikia albida*), sailfish (*Istiophorus platypterus*), longbill spearfish (*Tetrapturus pfluegeri*), Mediterranean spearfish (*T. belone*), and roundscale spearfish (*T. georgii*). However, the validity of the roundscale spearfish and its taxonomic relationship to the morphologically similar white marlin has only recently been resolved.

The white marlin was originally described by Poey in 1860, and with the exception of a generic reclassification (*Tetrapturus* to *Kajikia*; Colette et al. 2006), its validity has been accepted since the date of its description. The taxonomic status of the roundscale spearfish, however, has a long and convoluted history. Originally described by Lowe in 1840 from a specimen collected off the island of Madeira in the eastern Atlantic, the holotype no longer remains, and many of Lowe's manuscripts were lost in the 1874 shipwreck in which he lost his life (Robins 1974). The species status of the roundscale spearfish was questioned by Robins and de Sylva in 1960, who stated that its identity following Lowe's description, "will probably never be solved". Subsequently, Robins (1974) considered *T. georgii* to be a valid species, and compared the morphometric data and diagnostic characters of

the white marlin and the roundscale spearfish, as well as the longbill and Mediterranean spearfishes.

Robins (1974) presented diagnostic characters with which to differentiate white marlin and roundscale spearfish that include position of the anus relative to the first anal fin, presence or absence of spots on the dorsal fin, relative orbit diameter, and differences in scale texture and morphology. Robins also noted that the distribution of the roundscale spearfish was restricted to the eastern Atlantic; specimens he examined were from Sicily, the Strait of Gibraltar, and waters off southern Portugal. The validity of the roundscale spearfish was later corroborated by Shivji et al. (2006), using genetic analyses, scale morphology, and anus position, and the known distribution was extended to include the western North Atlantic.

The hatchet marlin, though never formally described, was recognized as being morphologically distinct from the white marlin due to the truncated appearance of its dorsal and anal fins (Nakamura 1985). Genetic analyses demonstrated that some fish classified as hatchet marlin were actually roundscale spearfish (Collette et al. 2006). Subsequent observations clarified that the truncated fin appearance is simply a morphological variation that occurs in roundscale spearfish and white marlin (Beerkircher et al. 2008).

There are relatively few studies on the biology of white marlin, and even fewer on the roundscale spearfish. The co-occurrence of these two species in the western North Atlantic, including the U.S. Mid-Atlantic Bight, has only recently been demonstrated. This co-occurrence complicates the results of past studies

considering that much of the biological information previously collected for "white marlin" in these waters likely includes both white marlin and roundscale spearfish. In the interest of creating effective management plans for each species, it is necessary to clearly distinguish one species from the other, while learning more about potential differences in the ecology and life histories of white marlin and roundscale spearfish. To obtain a better understanding of the ecology and morphology of white marlin in the Mid-Atlantic Bight, I used pop-up satellite archival tags to examine the movements and habitat utilization of known white marlin, as well as an analysis of scale morphology to determine if scale shape and squamation are valid characters useful for distinguishing white marlin and roundscale spearfish. Before describing those studies, I provide background information on white marlin biology, fisheries, and management.

White marlin biology

Due to the highly migratory nature and pelagic habitat of white marlin, little is known about their biology and ecology (Prince et al. 2005). White marlin are found throughout the Atlantic Ocean from approximately 45° N to 45° S, although they reach the farthest extremes of their range only in the respective warm season. They spend most of their time in the epipelagic zone, and they are frequently associated with areas of upwelling and weed lines, and spend time over geographical features such as drop-offs and canyons. White marlin are not known to school, but are frequently seen traveling in pairs or groups of three, and can

occasionally be seen in larger groups slashing their bills on the surface while preying on schooling fishes (Nakamura 1985).

White marlin and other istiophorids are opportunistic feeders. Analyses of stomach contents show that they frequently prey on squid (primarily *Loligo* spp. and *Illex* spp.) and bony fishes such as blue runners (*Caranx crysos*), dolphinfish (*Coryphaena hippurus*), flyingfishes (Exocoetidae), herrings (Clupeidae), pomfret (Bramidae), snake mackerels (Gempylidae), as well as small tunas and mackerels (Scombridae), among others (Nakamura 1985; Satoh et al. 2004; Hoolihan 2013).

The billfishes, including white marlin, are highly visual predators with eyes that are uniquely adapted to hunt for prey in the vast open ocean. Marlins spend a large proportion of daytime and nighttime hours close to the surface, in relatively warm and well-lit waters, although they do occasionally venture to greater depths (Hoolihan and Luo 2007; Horodysky et al. 2007; Goodyear et al. 2008). When making vertical excursions to colder and darker waters, marlin benefit from cranial endothermy. A highly specialized heating system located in the superior rectus eye muscle which lies beneath the brain and adjacent to the eyes, employs a countercurrent heat exchange originating at the carotid artery to maintain elevated tissue temperatures (Block 1986; 1987). Cranial endothermy results in improved visual temporal resolution, as measured by the flicker fusion frequency. A higher flicker fusion frequency at low ambient temperatures greatly increases the likelihood of detecting prey at low light levels (Fritsches et al. 2005).

White marlin exhibit sexually dimorphic growth, with females reaching larger maximum sizes than males, although the difference is not as pronounced as in blue marlin and black marlin. Female white marlin have been recorded at up to 281 cm in length and 82.5 kg in weight, while males remain smaller (Mather et al. 1972; Nakamura 1985). Age estimates of white marlin based on anal fin spines have ranged from one to as many as 13 years of age (Drew et al. 2006; Die and Drew 2008), while mark-recapture studies suggest that white marlin may live more than 15 years (Ortiz et al. 2003; Orbesen et al. 2008).

The examination of reproductive organs and larval sampling has provided insights into spawning locations and early life history characteristics. The size at which 50% of male white marlin are sexually mature (L_{50}) has been estimated at 139.0 cm lower jaw fork length (LJFL) (Oliveira et al. 2007). In females, L_{50} has been estimated at 149.0 cm, 160.4 cm, and to 189.9 cm LJFL (Oliveira et al. 2007; Arocha and Bárrios 2009; Arocha and Marcano 2006, respectively). White marlin are batch spawners, with fecundity estimates of 771,000-877,000 oocytes per female (Oliveira et al. 2007). During spawning seasons batches of 190,000-596,000 eggs may be fully hydrated at one time, and the timespan between batches averages 1.5 days (Arocha and Bárrios 2009).

White marlin are believed to spawn from April to July in the western central Atlantic, off the eastern coast of Florida, in the Windward Passage between the islands of Cuba and Hispaniola, and off the northern coast of Puerto Rico (Baglin 1979; Arocha and Marcano 2006; Arocha and Bárrios 2009). From May to June,

spawning occurs off the northeast coast of the Dominican Republic and in the vicinity of the Puerto Rico Trench (Prince et al. 2005; Arocha and Bárrios 2009). Spawning has been reported from June to July in the Gulf of Mexico (Rooker et al. 2012), and from December to March off northeastern and southern Brazil (Nakamura 1985; Arfelli et al. 1986; Oliveira et al. 2007). Oceanographic conditions conducive to white marlin spawning are poorly understood. However, one feature common to known spawning grounds is a region where two ocean fronts meet, causing mixing to occur between distinct water masses. These mixing zones contain characteristics of two water masses, and create a high concentration of plankton, which attracts larger predators (Laurs and Lynn 1977; Nakamura 1985; Schick et al. 2004; Arocha and Bárrios 2009). In this manner, oceanic fronts allow for an enhanced and localized food web that provides sufficient food for the spawning adults and their offspring, as well as providing passive larval transport out of the area by the movement of the front (Arocha and Bárrios 2009).

Larval and post-larval white marlin have occasionally been collected in plankton nets and dip nets, as well as being found in stomachs of tunas, billfishes, and other pelagic predators. As a consequence of their scarcity in traditional sampling gear, as well as challenges of larval billfish identification, little is known of their early life history stages (Prince et al. 2005; Luthy 2005). However, off the east coast of the Dominican Republic, larval blue marlin and white marlin caught in neuston tows in conjunction with histological analyses of adult ovaries confirmed

this as a spawning area in late spring (Prince et al. 2005). The larval period of white marlin is believed to be short due to rapid growth (Prince et al. 1991).

As mentioned previously, results of studies of white marlin sampled prior to 2006 are questionable as they may include data from the morphologically similar and recently validated roundscale spearfish. Landings of white marlin reported to the International Commission for the Conservation of Atlantic Tunas (ICCAT) include roundscale spearfish in significant numbers (SCRS 2012). Consequently, historical biological data and catch statistics of white marlin, including reproductive parameters, may not be accurate due to the unintentional inclusion of roundscale spearfish.

Fisheries

Worldwide there are no large scale commercial fisheries that target white marlin, although some small scale artisanal fisheries exist. White marlin, like all istiophorid billfish, are frequently caught as bycatch in pelagic longline fisheries, which target swordfish and tunas. A 2006 report from ICCAT estimated that the bycatch of white marlin in the tuna/swordfish longline fleet comprises approximately 90% of the total catch, but noted the lack of data from the artisanal fisheries. Historically, the reported catch of white marlin increased dramatically with the introduction of longline gear in the 1950s, and peaked at 4900 mt in 1965 (ICCAT 2012; 2013).

In 2011, the reported catch of white marlin in the Atlantic was 346 mt (321 mt landings and 25 mt discards), which was the smallest catch over the past ten years. Of the reported catch, Brazil had the highest amount of landings at 60 t, or approximately 22%. Venezuela was responsible for the second highest percentage of the catch at approximately 17%, or 47 mt. Other surface gears harvested 45 mt, and sport fishing catches were reported at 4 mt, of which 3 mt were from the North Atlantic (ICCAT 2012).

White marlin and the other istiophorids are highly prized as gamefish, and the recreational fishery is primarily catch and release. In the western Atlantic, the recreational fishery is concentrated along the east coast of the U.S., as well as off the coasts of Venezuela, Brazil, and many Caribbean islands. In the eastern Atlantic, recreational fishing efforts are concentrated off the west coast of Africa, the Canary Islands, and the Azores (Hoolihan 2013). White marlin are of minor economic value as a commercial food product, yet they are the basis of a recreational fishery that generates millions of dollars on the U.S. East Coast and other regions every year. Although recreational billfish fishing provides considerable financial benefits to many coastal communities on its own, billfish tournaments are extremely important economic drivers in the Caribbean, Gulf of Mexico, Mid-Atlantic Bight, and South Atlantic (Fisher and Ditton 1992). In 1989 dollars, nearly $180,000,000 were spent by U.S. recreational anglers in pursuit of billfish, including both tournament and non-tournament trips. Theoretically, this amounts to $4,242 per billfish caught, or $32,381 per billfish landed (Fisher and Ditton 1992).

A more recent study by the Maryland Department of Business and Economic Development's Division of Marketing & Communications evaluated expenditures by visitors during the 2009 White Marlin Open tournament in Ocean City, MD. The White Marlin Open was first held in 1974, and is a single billfish tournament that spans five days. In 2009, the benefit of the five-day tournament to statewide and local economies was estimated at $16 million dollars (Maryland DBED 2010). In addition, spending by tournament participants and spectators provided 130 jobs in Maryland, 70 of which were directly related to visitor expenditures during the tournament. The tax revenue for state and local government totaled $746,000. The White Marlin Open is one of four major white marlin tournaments in the Mid-Atlantic, with other leading tournaments taking place in New Jersey, Virginia, and North Carolina.

Management

In the United States, highly migratory species such as the billfishes, swordfish, and tunas are managed by the National Oceanic and Atmospheric Administration's (NOAA's) National Marine Fisheries Service (NMFS), under the authority of the Atlantic Tunas Convention Act (ATCA) and the Magnuson-Stevens Fisheries Conservation and Management Act. The ATCA implements recommendations for conservation and management adopted by the International Committee for the Conservation of Atlantic Tunas (ICCAT), which is the relevant

regional fisheries management organization for tunas and tuna-like species (such as billfish) in the Atlantic.

In 2000, ICCAT adopted its first mandatory management measure for white marlin and blue marlin which required all individuals captured alive in the pelagic longline and purse seine fisheries to be released in a manner that maximizes their survival. The measure also mandated a landings reduction of 67% for white marlin and 50% for blue marlin. Overall, Atlantic-wide landings decreased as expected, although some countries were unable to fully comply with the mandated reductions in landings. Management measures have resulted in a large number of live releases, but many vessels do not keep accurate records of these, and little information exists on survival of white marlin or blue marlin released from pelagic longline gear (Kerstetter and Graves 2006; Kerstetter et al. 2003). Thus, uncertainty remains as to post-release survival rates (ICCAT 2012).

Based on results of new stock assessments for white marlin and blue marlin, ICCAT further reduced total allowable catches for the two species and mandated country-specific quotas in 2012. The U.S. is currently limited to 250 Atlantic white and blue marlin (combined) annually. As of January 2011, the United States included roundscale spearfish in this count. For the 2013 fishing year, the United States reported recreational landings of 44 white marlin, 1 roundscale spearfish, and 55 blue marlin, totaling 99 of the allowable 250 fish (NOAA Fisheries 2014). The vast majority of white marlin caught in tournaments are released alive. However, in addition to awarding points for each release, some tournaments also award points

and prizes for the heaviest marlin. This requires anglers to land the largest animals for weighing. As a result, tournament landings account for most of the U.S. recreational landings of white marlin.

Domestically, the United States prohibits all commercial landings and trade of Atlantic istiophorid billfish. In the recreational fishery, NMFS encourages the live release of all billfish, and has implemented a minimum size of 63 inches LJFL for sailfish, 66 inches LJFL for white marlin and roundscale spearfish, and 99 inches LJFL for blue marlin. Longbill spearfish landings are not permitted. Fishermen are responsible for self-reporting any landings, except in registered billfish tournaments, in which tournament officials are required to report landings. Poor compliance with self-reporting outside of tournaments results in underreporting of recreational billfish landings. Additionally, there is likely misidentification of the catch, particularly in the case of the roundscale spearfish, for which reported landings remain very low.

In order to increase the likelihood of post-release survival in the recreational fishery, NMFS implemented a rule in 2007 requiring the use of circle hooks in natural baits for billfish tournaments. This ruling followed a study on post-release mortality of 40 white marlin tagged in the recreational fishery. Results showed that all white marlin caught on circle hooks survived, while only 65% of white marlin caught on "J" hooks survived (Horodysky and Graves 2005). Circle hooks necessitate different rigging and hooking techniques than "J" hooks when fishing for white marlin. Consequently, mandating the use of circle hooks in tournaments increased the

likelihood that fishermen would use circle hooks when fishing for white marlin outside of tournaments as well. This has resulted in increased post-release survival during tournament, as well as non-tournament fishing (Graves and Horodysky 2008).

Stock status

White marlin were petitioned for listing under the U.S. Endangered Species Act in 2001, 2006, and again in 2012. The 2001 and 2006 petitions were followed by status reviews, and NMFS concluded white marlin did not warrant threatened or endangered status at those times. Based on the information presented in the 2012 petition, NMFS determined that there was no need for a status review.

The most recent assessment for white marlin was conducted in 2012 by the ICCAT Standing Committee on Research and Statistics (SCRS) who concluded that the white marlin stock is likely overfished, but that overfishing is most likely not occurring unless catches are under reported (ICCAT 2012). The report states that relative fishing mortality has been declining over the last ten years. However, the report used two different models in the assessment, and each model produced a different result. The integrated model suggested that the white marlin stock can rebuild relatively quickly, while the surplus production model suggested that the stock will rebuild very slowly. Both approaches were considered equally plausible, and there was considerable uncertainty associated with the results: estimates of annual recruitment were uncertain, underreporting was believed to occur in the artisanal fisheries, and fishing mortality could have been greater than reported if

discards were not accurately reported. The presence of roundscale spearfish in unknown quantities created additional uncertainty for the white marlin stock status and outlook. Current catch levels are estimated at 400 t, a level of fishing mortality that will most likely result in an increase in stock size. However, the stock is unlikely to reach the biomass necessary to support maximum sustainable yield (B_{MSY}) in the next ten years (ICCAT 2012).

CHAPTER 2

Seasonal movements and habitat utilization

INTRODUCTION

Recent studies have shown that the relative abundance of white marlin and roundscale spearfish varies both spatially and temporally in the western North Atlantic. Beerkircher et al. (2008, 2009), and Arocha and Silva (2011) analyzed observer data from pelagic longline fisheries to estimate relative abundance of white marlin and roundscale spearfish in various areas of the western North Atlantic. Using fishing areas defined by NMFS, roundscale spearfish were caught in high relative abundance in the Northeast Distant area (NED), North Central Atlantic (NCA), Florida East Coast (FEC), and the Sargasso Sea (SAR). In the Northeast Coastal area (NEC), roundscale spearfish were caught in high relative abundance, particularly in the winter months (Beerkircher et al. 2008; Beerkircher et al. 2009). Roundscale spearfish were also found in high relative abundance in the northwest Caribbean Sea from April through December, with the highest abundance occurring in late summer and early fall. During January through March, however, roundscale spearfish were nearly absent from the northwest Caribbean, and white marlin dominated the catch (Arocha and Silva 2011).

On a local scale, genetic analysis of 21 years of tissue samples from "white marlin" (both white marlin and roundscale spearfish) weighed in at the Mid-Atlantic $500,000 billfish tournament indicates an increase in relative abundance of roundscale spearfish from the 1990s to the 2000s, as well as large annual variations over the last decade. It is important to note that for this tournament, fishing is

restricted to areas within 125 nmi of the Cape May sea buoy, and to the third week of August, and only the largest 5% of the fish are boated for weighing. For the 1992-2002 tournaments, only 5% of the "white marlin" brought to the weigh station were roundscale spearfish. From 2003-2013 this proportion increased to 29%, and in 2005 and 2010 more roundscale spearfish were weighed in than white marlin (71% of 14 fish and 57% of 30 fish, respectively; Graves and McDowell, unpublished data). The 2012 Mid-Atlantic $500,000 tournament was the first since 2000 in which no roundscale spearfish were landed. Two weeks earlier however (at the White Marlin Open in Ocean City, MD) 38% (i.e., 3 out of 8) of the "white marlin" weighed in were roundscale spearfish. Mitochondrial DNA analysis of "white marlin" weighed in at the White Marlin Open in 2007 and 2008 indicated that 31% of the individuals were roundscale spearfish (Beerkircher et al. 2009).

Although tournament results show annual variation in the ratio of roundscale spearfish to white marlin landed, using these numbers to estimate relative abundance of the two species for the area and year may lead to biased results. As noted above, in both tournaments, fishing is restricted to a limited area during a single week each year, and only the largest fish are landed. Many fishermen report that most roundscale spearfish caught in the recreational fishery tend to be larger than the "typical" white marlin. Since the weigh station data represent only the largest individuals, very little is known about the relative abundances of smaller, younger white marlin and roundscale spearfish. Most recreational fishermen do not understand or acknowledge the difference between the two species, and of those

who are aware of the differences, few take the extra time required to bring a hooked fish next to the boat to allow identification before release. To improve our understanding of the relative abundance of white marlin and roundscale spearfish of all sizes, an objective of my study was to gather catch data from recreational fishermen, and to use these data to estimate the relative abundance of white marlin and roundscale spearfish of all size classes available to the fishery in the Mid-Atlantic Bight throughout an entire season.

Movements of istiophorid billfishes have been studied with various technologies including active tracking using ultrasonic telemetry, conventional tagging and more recently, pop-up satellite archival tags (PSATs). Active tracking of pelagic fishes is logistically challenging due to the difficulties of continuously following a free-swimming fish from a small vessel for hours to days in variable sea conditions. Conventional tagging necessitates recapture of the tagged fish, and return rates of conventionally tagged billfishes typically have been less than 2%. This low return rate of conventional tags has been attributed to tag shedding, low reporting rates from various regions and fisheries, and the wide dispersal abilities of the fish (Ortiz et al. 2003).

A review of various billfish tagging programs from 1954-2003 accounted for 317,073 conventionally tagged billfishes (Ortiz et al. 2003), none of which was recorded as a roundscale spearfish. This illustrates the issue that prior to 2006 it is possible that roundscale spearfish may have inadvertently been tagged and included in the analyses with white marlin or another billfish, such as longbill spearfish. Of

the 42,379 conventional tags placed on white marlin, approximately 2% have been recovered and reported. Data from these tags show only the minimum straight-line distances travelled. A compilation of conventional tagging data shows that the longest recorded distance travelled by a white marlin was 6517 km after 141 days at large (Ortiz et al. 2003). The movement of this fish was trans-Atlantic, from the east coast of the United States to the west coast of Africa. Although several trans-Atlantic movements have been documented, white marlin have not been documented outside of the Atlantic Ocean, and accordingly, no trans-oceanic movements have been recorded (Ortiz et al. 2003).

White marlin tagged with conventional tags and later recovered have tended to be at liberty for longer periods of time than other istiophorids, with 30% of the recovered fish being at large for 2 – 15 years (Ortiz et al. 2003). Movement of considerable numbers of white marlin has been noted between the U.S. East Coast, the Gulf of Mexico, and Venezuelan waters indicating substantial connectivity between these regions. The locations and timing of the release and recovery points of white marlin, combined with their relatively long time at liberty compared to other billfishes, suggest seasonal site fidelity (Ortiz et al. 2003; Jaen and Jaen 1994); however, detailed data to substantiate this hypothesis are lacking.

PSATs have also been used to study movements of white marlin. The advantage of PSATs over conventional tags is that fish do not have to be recaptured as the tag releases from the fish on a programmed date or after a specified length of time, and then transmits the archived data to the Advanced Research and Global

Observation Satellite (ARGOS) satellite system. Many newer models of PSATs collect geolocation data. However, most PSAT models used on white marlin to date have only provided location data for the site of tag deployment and the location of tag release (i.e., after it begins to transmit). The movement information obtained from these PSATs is thus similar to that of recovered conventional tags: a minimum straight line distance traveled by the fish between the point of release and recovery.

The vast majority of PSAT deployments on white marlin have been for limited duration (5–10 days), and have primarily been used to investigate post-release mortality. Movements have been examined for white marlin tagged along the U.S. East Coast, in the northern Caribbean, and off Venezuela. The data showed minimum straight line distances from 30 to 1171 km from the point of release. There was, however, no evidence of connectivity between the three regions (Horodysky et al. 2007). Prince et al. (2005) used PSATs to study movements of six white marlin tagged off the Dominican Republic (for 28-37 days) during the spring spawning season. Despite the longer deployment duration, the minimum straight line distance from tagging to the location of tag release still only ranged from 59 to 496 km.

To obtain more detailed information about the movements of white marlin during the time they are tagged, my second objective was to use light-based geolocation to examine the timing of movements out of and back into the Mid-Atlantic Bight, to identify overwintering areas, and investigate possible use of reported spawning grounds.

In addition to providing information on the movements of white marlin, PSATs have greatly improved our understanding of habitat utilization due to the tag's ability to record temperature and pressure (a proxy for depth) throughout the duration of tag deployment. Similar to studies of white marlin movements, previous investigations of white marlin habitat utilization have primarily used information from short-term tag deployments. Two separate studies in which marlin were tagged in multiple locations suggest that habitat utilization varies between different geographical regions, with observed differences in depth and temperature occupied by the different groups of fish (Horodysky et al. 2007; Dutton 2010). Although these studies demonstrated differences in habitat utilization by region, it is not clear whether the differences were due to varying oceanographic conditions, prey availability, etc., or individual variability. My third objective was therefore to analyze the habitat utilization of white marlin for longer periods, noting the responses of individual fish as they encountered different oceanographic conditions resulting from their movements or due to seasonal change.

MATERIALS AND METHODS

Pop-up Satellite Archival Tags

Habitat utilization and movements of white marlin in the western North Atlantic were studied using Microwave Telemetry PTT-100 standard rate PSATs. Tags deployed in 2011 were programmed to release after 12 months, while tags deployed in 2012 were programmed for pop-off after six months. PTT-100 PSATs recorded temperature, pressure (used as a proxy for depth), and light levels for light-based geolocation. These sensors were hermetically sealed within a low-drag housing of composite carbon. The tags were 16.6 cm in length with a 17 cm antennae, a maximum diameter of 4.1 cm, and were positively buoyant with a mass of approximately 66 g in air.

The tags were programmed to record data every 15 minutes during the first four months of deployment, every 30 minutes during months 5-8, and hourly during months 9-12. More recently collected data overwrote portions of the earlier, more frequently recorded data. Tags were programmed to release from the fish when one of the following occurred: the allotted time period was reached (six or 12 months in this study), the tag spent four days at a constant pressure (constant pressure is considered to be equivalent to a depth variation of less than 20 m), or the tag reached a pressure rating of 3000 psi (approximately 2100 m depth) (http://www.microwavetelemetry.com/constantdepth.cfm). The release

mechanism was an electro-corrosive wire could be triggered by any of the previously mentioned events. In order to conserve battery life after release from the fish, and therefore maximize data transmission from the tag to the ARGO system, the PTT-100 tags used Satellite-in-View technology (SiV™), which limited transmissions to times when there was a high probability that a satellite is in view above the horizon.

Tags were rigged with a tether of approximately 16 cm, made of 200 pound test monofilament fishing line, which was looped through a surgical grade nylon dart-shaped anchor on one end and the PSAT on the other end, and was crimped back to itself on both ends. The crimps and monofilament ends were covered in heat shrink tubing to minimize abrasion against the fish's body (Graves et al. 2002).

Relative abundance estimates and tagging

To create a database for estimating temporal patterning and relative abundance of roundscale spearfish and white marlin during their period of greatest abundance in the mid-Atlantic region (summer and fall), I arranged for cooperating recreational fishermen from private and charter boats to collect data on fish they caught. Laminated sheets illustrating the morphological differences between the two species (Appendix 1), as well as data sheets for the catch data, were distributed. I requested information only for roundscale spearfish and white marlin that could be positively identified. The data requested included species, date, approximate geographical location, and estimated weight of the fish.

White marlin tagged for this project were caught on cooperating private and charter recreational fishing boats in the U.S. Mid-Atlantic Bight with dead bait and circle hooks. After the fight, fish were brought alongside the boat and left in the water. The mate steadied the fish by holding their bill and dorsal fin while they were tagged. This allowed for optimal tag placement. I employed a tagging pole to insert the tag anchor into the dorsal musculature below the highest point of the dorsal fin, following the method of Graves et al. (2002). Insertion into this region allows the tag anchor to interlock with the pterygiophores, securing the tag in place, while keeping the nylon anchor safely above the body cavity. While alongside the boat, length and/or weight were estimated. The condition of the fish, fight time, and fighting behavior were noted, as well as the GPS coordinates (i.e., location) and depth. To ensure the best possible survival rate, fish that were unable to maintain an upright position alongside the vessel were revived by holding them underwater alongside the boat while moving ahead slowly to force ventilate them.

Data analyses

The PT-100 tags collected light level data for each day they remained attached to fish, and movements of fish were inferred using the light-based geolocation method (described in detail by Metcalfe 2001; Musyl et al. 2011). Light level data were used to determine times of sunrise and sunset (i.e., day length, from which latitude was estimated) and the times of local noon (from which longitude was estimated). The latter is much more accurately estimated than the former,

because only the midpoint of the day is needed and potential errors in the time of sunrise and sunset will generally offset each other. At low latitudes or during the equinoxes, the estimates of latitude are much less accurate, due to uniformity of day length (Metcalfe 2001; Musyl et al. 2011). Thus, geolocation data from dates around the equinoxes were excluded from the analyses.

Geolocation data were analyzed with R statistical software (R Core Team 2013) to estimate the timing and direction of movements of white marlin, using the package analyzepsat (Galuardi 2012) and the Unscented Kalman Filter Sea Surface Temperature (UKFSST) model (Lam et al. 2008). The Kalman filter (Harvey 1990) is a linear quadratic estimation (LQE) that utilizes an algorithm commonly used for navigation. This algorithm uses sequential measurements observed over a period of time, eliminates noise, and generates more precise estimates than could be determined from a single measurement. Originally the Kalman filter was used in combination with a state-space statistical model (Sibert and Fournier 2001) to estimate a "most probable" track, and this approach was widely adopted (Musyl et al. 2003; Sibert et al. 2003; Wilson et al. 2005). This model was later extended to incorporate sea surface temperature (Nielsen et al. 2006) and was made available as the KFSST package (Nielsen and Sibert 2005). Lam et al. (2008) presented a refinement on the previous model by using the unscented Kalman filter (Julier et al. 2000) with a state-space model. The unscented Kalman filter is an improvement on the basic Kalman filter due to its ability to handle non-linearities, and is an improvement on the KFSST model because the smoothing of the sea surface

temperature field is included within the model. Consequently, measurement error estimation occurs within the model, resulting in the avoidance of prior assumptions for longitude, latitude, and SST estimate accuracy (Lam et al. 2008). Previously, when using KFSST, it was necessary to arbitrarily determine the smoothing a priori, which created problems in the case of missing observations and outliers. Due to the inclusion of sea surface temperature (SST) smoothing in this newer model, it can be tailored to the regional oceanographic conditions for more accuracy (Lam et al. 2008).

For my analyses, I focused specifically on when white marlin leave the mid-Atlantic, where they go, the route they take to get there, and how synchronized movements are among individuals. I planned to specifically compare any "doubles" (fish that were caught at the same time, and therefore tagged together) to determine if movements of the pairs match more closely than two marlin tagged at different times or on different days. Maps to show the white marlin movements were prepared in ArcGIS 10 (Esri, Redlands, CA).

Habitat utilization data were illustrated for visual analysis as histograms of time at temperature and time at depth. The ranges in daily temperatures experienced by the fish were examined by comparing the sea surface temperature (SST) (inferred to be the daily maximum) to the daily minimum temperature following Brill et al. (1999). Data points from before tag deployment and after pop-up were excluded from all analyses.

To investigate potential diel differences in habitat utilization of white marlin, I examined depth and temperature means throughout the day/night cycle. Six hour periods of day and night were chosen, and means were calculated for each of these hours. Daytime was defined as three hours before and after the midpoint between sunrise and sunset, and nighttime was defined as three hours before and after the midpoint between sunset and sunrise. Crepuscular periods were omitted from these analyses. Means of vertical excursion depths and temperatures were graphed separately for daytime and nighttime to illustrate possible differences in habitat utilization. To further examine these differences, a linear mixed effects model was used. The data were found to be non-normal, and were Box-Cox transformed before analysis. Following the manner of Graves et al. (2009) and Howey-Jordan et al. (2013), differences in depth and temperature means between time periods were assessed with a linear mixed effects model with repeated measures:

$$Y_{ij} = \mu + \beta_j + \alpha_i + \varepsilon_{ij}$$

μ = the overall mean of depth and temperature
α_i = the random effect due to individual fish
β_j = the fixed effect of diel period j
ε_{ij} = error terms ($\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$)

A repeated measures analysis was necessary due to the correlation of the replicates in the data set, since multiple observations were from the same individuals. The repeated measures model accounts for correlated data, by assuming non-independence of replicates. Following Graves et al. (2009) and

Howey-Jordan et al. (2013), covariance structures were fitted to the data and evaluated on Akaike's information criterion (AIC), and the best fitting covariance structure for both depth and temperature was found to be the autoregressive moving average (ARMA). Analyses were performed in SAS (MIXED procedure, vers. 9.3, SAS Inst., Inc., Cary, NC).

RESULTS

Relative abundance estimates

Catch records of white marlin and roundscale spearfish returned by captains and crew on private and charter recreational fishing vessels in the Mid-Atlantic Bight were used to estimate the relative abundance of the two species. Data sheets and identification guides were handed out to approximately 70 individuals, and reports were received from eight. Based on those records, catches of 327 white marlin and 13 roundscale spearfish, and 481 white marlin and 2 roundscale spearfish were reported in 2011 and 2012, respectively. Combining both years, roundscale spearfish accounted for less than 2% of reported catches.

Tagging

I spent 19 days at sea during the 2011 field season during which I tagged three fish, and nine days during the 2012 field season, during which I tagged nine fish. My project began as a comparative study of the movements and habitat utilization of roundscale spearfish and white marlin. However, midway into the second field season (2012) it became apparent that I was not going to be able to encounter enough roundscale spearfish to complete the study. At that point, in consultation with my committee, I changed the objectives of my tagging project to focus solely on white marlin, and in just a few days, I was able to deploy the remaining tags.

All PSATs were deployed on adult fish. Fishing trips left from ports in Virginia Beach, VA, or Cape May, NJ. A total of 12 PSATs were deployed, three were programmed to release after 12 months, and nine after 6 months. All three 12-month PSATs were deployed in August and September 2011, two on white marlin and one on a roundscale spearfish. The remaining nine tags were deployed on white marlin in September of 2012 (Table 1). All white marlin were tagged in the vicinity of the Norfolk Canyon (n=11), while the roundscale spearfish was tagged between the Lindenkohl and Spencer canyons

Fight times from hook-up to tagging ranged from 6-31 minutes (mean=16, *SEM*=2). All fish were caught on naked ballyhoo (no lure attached), and were hooked in the corner of the lower jaw (n=6), lower jaw (n=3), palate (n=2), or gut (n=1). After being brought alongside the boat, fish were evaluated for activity level, color, body positioning, stomach eversion, and bleeding. Individuals were given an overall condition score based on 10 points. The condition of the 12 tagged fish ranged from 6.5 to 10 (mean = 7.7, SEM = 0.4). Only one fish (WHM 1) everted its stomach after being hooked in the gut. The stomach was not lacerated, and this fish survived the hooking event and carried the tag for 325 days. Bleeding was observed in only two fish. Both bled lightly and locally; WHM 9 bled at the location of hook in the lower jaw, and WHM 11 bled at the insertion point of the tag dart. These fish both survived the fishing and tagging events, and carried the tags for 180 and 103 days, respectively. Seven of the 12 fish were resuscitated alongside the boat for 1-4

minutes while moving forward at 3-4 knots, a common practice in the recreational fishery.

Ten of the 12 PSATs (83%) reported data through the ARGOS satellites, while two PSATs (both attached to white marlin) did not report. Five of the seven tags programmed to remain attached for six months (72%), and two of the three tags programmed to remain attached for 12 months (66%) released before the programmed pop-off date (Table 2). Of the tags that released prematurely, six released after experiencing constant pressure, and one tag released after exceeded the programmed maximum depth limit. The 12-month tags remained attached for periods of 34, 325, and 365 days (mean=180; *SEM*=127), and the 6-month tag attachments ranged from 8-180 days (mean=113; *SEM*=22). The percentage of data transmitted through ARGOS system ranged from 84-100% (mean=92%; *SEM*=2) (Table 2). All 10 fish showed habitat utilization consistent with survival in the days after release.

Seasonal movements

Light-based geolocation can provide only one set of longitude and latitude coordinates per day, so distances traveled were calculated as straight line distances between estimated geolocations (which were not obtained every day for each individual). In addition to the error associated with light-based geolocation, distance traveled was also likely underestimated because fish most likely did not travel in straight lines. In some cases there was less than one geolocation data point each

day. This could have resulted from a less than 100% reporting rate of the data to the satellite, or due to the occurrence of a vernal or autumnal equinox during the fish's time at liberty.

Figure 1 shows light-based geolocation estimates for the tracks of all white marlin, with each color representing the track of a different fish. To illustrate the time of year during which these movements took place, as well as to show areas frequented throughout the tagging duration, Figure 2 shows the geolocation-based estimates of all white marlin combined, with colors indicating the month for each individual position. Cooler colors show movements during the colder months, while warmer colors show movement during the warmer months.

WHM 1 was tagged on August 13, 2011 (Figure 3). This fish moved along the U.S. East Coast, as far north as southern New Jersey and as far south as northern Florida throughout the fall, winter, and early spring. During this time spent along the East Coast, this fish traveled approximately 8763 km at an average speed of 32.8 km/day or 1.4 km/hr. WHM 1 left the Mid-Atlantic Bight on May 11, and traveled approximately 1457 km almost due eastward, past Bermuda. During this directed eastward movement, the fish traveled approximately 63.3 km/day or 2.6 km/hr. This was considerably faster than the rate of speed it traveled along the U.S. east coast. WHM 1 remained in this general area, in which it reached the farthest point from the U.S. East Coast, through the end of June. The tag exceeded its maximum depth limit and released from the fish on July 1, 2012 (325 days after release) at a

point 342 km northeast of Bermuda. Overall, WHM1 traveled a total of 10820 km, at an average speed of 33.3 km/day or 1.4 km/hr.

WHM 2 was tagged on September 11, 2011, and the tag remained attached for the full programmed duration of 365 days. The fish left the Mid-Atlantic Bight on September 26, just two weeks after being tagged (Figure 4). It traveled in a predominately southeasterly direction, ending up approximately 1137 km north of Brazil on December 18. During this passage the fish traversed approximately 4929 km at an average speed of 78.2 km/day or 3.26 km/hr. This was among the highest average speed I observed. WHM 2 spent nearly four months north of Brazil, which included the farthest point it reached from the U.S. East Coast. Leaving this area in mid-April of 2012, the fish began a northwesterly course toward the Windward Islands of the Lesser Antilles, entering the chain of islands near Barbados on a track to the south of the route it took on the way east. The fish then continued northwest, staying close to the Leeward Islands before moving westward to the Greater Antilles, passing north of Puerto Rico and the eastern half of the Dominican Republic, before heading northward into deeper waters on approximately June 30, 2012. The fish then made a directed movement to the northwest, returning to the Mid-Atlantic Bight on approximately July 24, 2012. This directed movement covered approximately 2562 km at an average speed of 106.75 km/day or 4.45 km/hr. This was the fastest rate of speed I observed. The PSAT released from the fish only 445 km east of the tagging location. Overall, WHM2 traveled approximately 22846 km over a 365-day period at an average speed of 62.6 km/day or 2.6 km/hr.

WHM 3 was tagged on September 1, 2012, and left the mid-Atlantic Bight approximately two weeks later (September 15, Figure 5). This fish travelled almost due east for 822 km, at an average speed of 68.5 km/day or 2.85 km/hr, before turning south near the end of September. It continued south through approximately November 7, when it reached the waters just north of the Dominican Republic. During this time period, the fish traveled approximately 1908 km, at an average speed of 45.4 km/day or 1.9 km/hr. It spent the rest of November and most of December north of Hispaniola, crossing back and forth from the east side of the island north of the Dominican Republic to the west side, north of Haiti. During this time it traveled approximately 1346 km at a speed of 27.5 km/day or 1.1 km/hr. The tag released due to constant pressure (at the surface) on December 27, 2012, north of Haiti. Over a period of 117 days, WHM 3 traveled approximately 4444 km, at an average speed of 38.6 km/day or 1.6 km/hr.

WHM 4 was also tagged on September 1, 2012, and traveled almost due east, before heading south, then west, back east, and south again (Figure 6). The fish began a directed movement south on approximately November 10, and continued through the Mona Passage, between the Dominican Republic and Puerto Rico. During this transit, the fish traveled approximately 2174 km, at an average speed of 103.5 km/day or 4.3 km/hr. From the Mona Passage this fish continued south to waters off the coast of Aruba eventually reaching northern Venezuela by January 2013. The fish then moved slightly westward, and spent the month of February just north of Colombia. The tag released after the programmed time

period of 180 was reached (March 1, 2013). Over this time period, WHM 4 traveled approximately 13603 km at an average speed of 75.5 km/day or 3.2 km/hr.

WHM 5 was also tagged on September 1, 2012 (Figure 7). This fish spent the month of September traveling off the coasts of Virginia, and North and South Carolina. The tag released prematurely on October 8, 2012, off the North Carolina coast after only 38 days at liberty. The geolocation data had large gaps due to the Autumnal Equinox, which occurred in the middle of the fish's relatively short track. WHM 5 traveled 2859 km over 38 days, at an average speed of 75.24 km/day or 3.13 km/hr.

WHM 6, 7, and 8 were all tagged on September 2, 2012. The tag on WHM 6 did not report. WHM 7 left the Mid-Atlantic Bight approximately one week after it was tagged, moving south, then east, and slightly north (Figure 8). Beginning on September 19, the fish made a more directed movement south and arriving just east of the Turks and Caicos Islands on October 13. During this period the fish traveled approximately 1652 km at an average speed of 68.8 km/day or 2.9 km/hr. It then continued south to coastal waters north of Haiti, before traveling through the Windward Passage between Cuba and Haiti, and then west toward Jamaica. The tag released prematurely on October 31, 2012 just east of Jamaica. WHM 7 traveled approximately 4453 km over 58 days, moving at an average speed of 76.8 km/day or 3.2 km/hr.

WHM 8 spent its first week at liberty in the Mid-Atlantic Bight off the coast of Virginia, moving as far north as New Jersey (Figure 9). On September 10, 2012 (eight

days after tagging, the tag (and most likely the fish) were presumably preyed upon, as the transmitted data indicated catastrophic damage to the pressure sensor. After the inferred predation event, the tag reported unrealistic pressure readings that corresponded to depths ranging from 86 m above sea level to 1285 m below the surface. The temperature readings during this time were relatively stable. Over a period of nine days prior to the presumed predation event, WHM 8 traveled approximately 835 km, at an average speed of 92.8 km/day or 3.9 km/hr, which was among the fastest rates of speed in this study.

WHM 9 was tagged in the Norfolk Canyon on September 7, 2012, and spent nearly two weeks off the coast of Virginia and North Carolina (Figure 10). On September 21, the fish began a directed southward movement to just north of the Dominican Republic, arriving October 29. During this period the fish traveled approximately 2863 km at an average speed of 75.3 km/day or 3.1 km/hr. It then moved through the Mona Passage (between the Dominican Republic and Puerto Rico) and continued south to coastal waters north of Venezuela, where it remained until February 11. The fish then began a westward track (passing north of Colombia), before moving northwesterly toward Jamaica. The tag reached its programmed pop-off date on March 7, 2013 (180 days after deployment) and began reporting approximately 114 km southeast of the eastern tip of Jamaica. WHM 9 traveled approximately 11,381 km during the 180 days at liberty, at an average speed of 63.2 km/day or 2.6 km/hr.

WHM 10 and 11 were both tagged in the Norfolk Canyon on September 16, 2012. The fish were caught together and tagged together, but the tag from WHM 10 did not report. WHM 11 began moving south along the continental shelf within a few days of being tagged (Figure 11). On September 21 (while in coastal waters offshore of the North Carolina/South Carolina border), the fish began moving offshore and to the south, and eventually reached Bahamian waters on November 5. From the time the fish left coastal Carolinian waters to when it entered Bahamian waters, this fish traveled approximately 1742 km, averaging 36.3 km/day or 1.5 km/hr. The fish then continued south to waters north of central Cuba, before moving north again to northern Bahamian islands (Grand Bahama Island, Abaco, Eleuthera, and Andros Islands), where it spent most of November and early December. The tag released prematurely on December 23 as the fish was moving north off the Florida coast. Over the 103 days at liberty, the fish traveled approximately 5099 km at an average speed of 49.5 km/day or 2.1 km/hr.

One PSAT was deployed on a roundscale spearfish (SPG 1) caught in waters between the Lindenkohl and Spencer Canyons on September 10, 2011 (Figure 12). The fish moved out of the Mid-Atlantic Bight on September 26th, initially to the southeast then nearly due east for approximately 1317 km. The tag released prematurely on October 14th, 2011, after 34 days at liberty. During this time, fish traveled 1317 km at a speed of 38.7 km/day or 1.8 km/hr.

Over all fish, mean swimming speeds ranged from 39-93 km/day or 1.6-3.9 km/hr.

High use areas for the white marlin included in this study were the Mid-Atlantic Bight, and the U.S. East Coast from Florida to New Jersey (Figure 2). Fish in these areas generally stayed close to the continental shelf, and along the offshore canyons. High use areas outside the Mid-Atlantic Bight included waters around Hispaniola, where five of the nine white marlin were tracked. Two of these fish traveled through the Mona Passage between Hispaniola and Puerto Rico. WHM 2, 4, and 9 all spent time between various Caribbean islands and the South American coast.

In addition to occupying common areas, several of the white marlin took similar paths leaving the Mid-Atlantic (generally in September). The fish traveled offshore, before turning and making a directed movement to the south. WHM 2, 3, 4, 7, 9, and 11 all followed this general path. WHM 4 and 9 continued their southern movement through the Mona Passage, while WHM 7 used the Windward Passage to move south of the Caribbean islands. WHM 11 used a slightly different path, moving west toward the Bahamas after its southern movement. WHM 1 exhibited an atypical movement pattern. Tagged for 325 days, this fish remained along the continental shelf for the fall and winter, and only moved eastward in the spring. The tags for WHM 5 and 8 released before these fish exited the Mid-Atlantic, and therefore, there is no information on their long-range movements.

Of the pairs of white marlin caught and tagged together, WHM 3 and 4 were the only pair for which both tags reported. These two fish had similar overall movements, as they both moved east out of the Mid-Atlantic and then began

directed movements to the south. WHM 3 turned west above Hispaniola before losing its tag, while WHM 4 continued south through the Mona Passage before its tag released between Haiti and the Colombian coast. Although these movements were similar, the timing was not coincident, and it is highly unlikely that they were moving together.

Utilization of the water column

White marlin generally associated with the upper half of the epipelagic zone (0-100 m), with 97% of all depth records falling within this range, and 75% of time spent in the top 10 m (Figure 13). The mean depth of white marlin was 26 m (*SEM*=0.1), and the mode was 0 m. Maximum depth reached by a white marlin was 226 m.

Temperatures occupied ranged from 12-30˚C, with a mean of 26˚C (*SEM*=0.009). Pooled data for all fish showed 21% of their time was spent between 20-24˚C, with 63% of the time spent between 24-28˚C. For all white marlin approximately 98% of their time was spent within 8˚C of the SST (Figure 14).

The one roundscale spearfish tagged had an even greater association with surface waters, spending 99.7% of its time in the top 100 m, and 74.7% of its time in the top 10 m (Figure 15). Mean depth for this fish was 15 m (*SE*=0.5). The mode was 0 m, and maximum depth was 161 m. Temperatures inhabited by the roundscale spearfish ranged from 22-29˚C with a mean of 26˚C (*SE*=0.02). The roundscale spearfish spent 7.3% of its time in temperatures of 20-24˚C, and 87% in

temperatures of 24-28˚C. This fish spent all of its time within 6 degrees of the sea surface temperature, and 88% of its time within 4 degrees of SST.

The tracks of two white marlin, WHM 1 and WHM 2 (Figures 3 and 4) which carried tags for 325 and 365 days (respectively) were divided into segments according to season and geographical location. This allowed me to examine possible differences in habitat utilization among individual white marlin throughout different seasons, geographical regions, and oceanographic conditions.

Habitat utilization for WHM 1 was separated into three segments. This fish was tagged in August of 2011, and remained in the waters off the U.S. East Coast until May 11, 2012. During this period, it spent 62% of its time in the upper 10 m of the water column, and 98% of its time in 0-100 m. Only 2% of its time was spent at depths greater than 100 m. However, a large portion of the time this fish spent along the U.S. East Coast was spent over the continental shelf where water depths greater than 100 m were unavailable. During this segment the fish spent only 27% percent of its time at 24-28˚C, and a greater proportion of its time (69%) was spent at cooler temperatures of 20-24˚C (Table 3, Figure 16B). When moving due east toward (and then past) Bermuda from May 11 to June 8, time at depth was similar to the previous segment, but with less time spent in the 0-10 m zone (55%). During this directed movement, 96% of the fish's time was spent in the top 100 m, and 3.4% in waters deeper than 100 m. The fish spent only 7.2% of its time at24-28˚C, and 82% at 20-24˚C (Figure 16C).

In the last segment of the track (June 8-July 1), WHM 1 remained within a relatively small area east of Bermuda. During the last segment, WHM 1 spent 50% of its time in the surface waters of 0-10 m, and slightly more time at 0-100 m compared to either of the other segments (98.3%). And although WHM 1 spent slightly less time (1.7%) at depths greater than 100 m, it spent more time in cooler water than in other segments, with 80% of time spent in 20-24˚C, and only 18% in waters with temperatures of 24-28˚C (Table 3).

WHM 2 was tagged on September 11, 2011, and remained in the Mid-Atlantic Bight until September 25. During this time period along the continental shelf, this fish spent 50% of its time in 0-10 m, and 98% of its time in the upper 100 m, leaving only 2% of time for depths greater than 100 m. In this region, WHM 2 spent 71% of its time in waters of 24-28˚C, and 22% in cooler waters of 20-24˚C (Figure 18A).

WHM 2 conducted a southeastward movement out of the Mid-Atlantic Bight from September 26 until December 18. During this period, the fish spent 47% of the time in surface waters of 0-10 m, and 96% of the time in the top 100 m. Approximately 38% of the time was spent between 50-90 m, and only 4.1% of its time at depths greater than 100 m. This fish spent 11% of the time in waters of 20-24˚C, and 86% of the time in waters of 24-28˚C (Figure 18B). During the time spent in a relatively small area off the northern coast of Brazil (December 19-April 15), the fish spent 54% of its time in the surface waters (0-10 m), and 99% in the top 100 m. Only 1.2% of the time was spent at depths greater than 100 m. During this period,

the fish spent 1% of its time in water temperatures of 20-24˚C, and the remainder (99%) between 24-28˚C (Figure 18C).

During the next segment (May 18-June 22 when it was traveling through the Caribbean Islands), this fish spent only 28% of its time in surface waters of 0-10 m and 81% of its time shallower than 100 m. Compared to the other segments of its track, the fish spent a much larger percentage of its time (19%) at depths greater than 100 m. This time period had a greater range of temperatures than the previous segments, and the fish spent 3.2% of its time in waters of 20-24°C, and 80% in waters of 24-28˚C (Figure 18D).

Throughout the last segment of the track, WHM 2 undertook a directed movement from the Caribbean to the Mid-Atlantic Bight (June 22-July 15). During this period, the fish spent 29% of its time in surface waters of 0-10 m, nearly half of its time (49%) between 50-90 m, and 99% of its time in the top 100 m. Only 1.1% was spent in depths greater than 100 m. During this segment the fish spent 44% if its time at 20-24˚C, and 45% at 24-28˚C. The temperature range experienced during this segment (20-30˚C) was, however, the largest among the four segments. Over the entire 12 months during which WHM 2 was tagged, it spent 47% of its time in surface waters of 0-10 m, 34% of its time at 40-90 m, and 96.5% of its time between 0-100 m. It spent less than 4% of its time at depths greater than 100 m. Overall, 5% of this fish's time was spent in temperatures of 20-24˚C and 63% in waters of 24-28˚C.

To compare habitat utilization across fish in different regions, all observations were pooled for time spent along the U.S. East Coast (n=9 fish; n=18489 depth observations; n=18774 temperature observations). Similarly, all observations were pooled for time spent in the vicinity of the Dominican Republic (n=5 fish; n=20213 depth observations; n=20519 temperature observations). White marlin along the U.S. East Coast spent 58% of time in the 0-10 m stratum, while 99% was spent in the upper 100 m. This could be due, in part, to the limited depths available along the continental shelf. These fish spent only 1.3% of their time below 100 m. East Coast fish spent 48% of their time in waters of 20-24˚C, and 48% of their time in waters of 24-28˚C. In the Caribbean, white marlin spent 44% of their time in the surface waters (0-10 m), and 95% of time in 0-100 m. Less than 5% of time was spent at depths greater than 100 m. In the Caribbean, 48% of time was spent in cooler temperatures of 20-24˚C, and 47% was spent in waters of 24-28˚C.

Depth data for all white marlin were pooled to investigate differences in daytime and nighttime habitat utilization. During the day fish spent 26% of their time in surface waters of 0-10 m, 80% in 0-60 m, 96% in the upper 100 m of the water column, and only 4% at depths greater than 100 m. In contrast, during nighttime hours the same fish spent 88% of their time at the surface, 99% in the upper 60 m, and more than 99% in the upper 100 m. Only 0.1% of time was spent at depths greater than 100 m.

During daytime hours fish spent 32% of their time in temperatures of 20-24˚C, with 63% spent in temperatures of 24-28˚C. The minimum daytime

temperature recorded was 14.6˚C, and maximum was 29.7˚C. During nighttime hours 68% of their time was spent in temperatures of 24-28˚C, and only 17% between 20-24˚C. The minimum temperature recorded during the nighttime was 18.9˚C and the maximum was 29.7˚C (Figure 19).

A repeated measures linear mixed effects model indicated a significant difference in diel habitat utilization in regard to depth ($p<0.001$) and temperature ($p<0.001$), with the tagged white marlin spending time at greater depths and cooler temperatures during the day (depth: 37.6 m, CI [35.4, 39.8 m]; temp: 25.5 ˚C, CI [25.3, 25.6 ˚C] than at night (depth: 2.30 m; CI [0.08, 4.51 m], temp: 26.7 ˚C, CI [26.6, 26.9 ˚C], where CI designates the upper and lower limits of the 95% confidence interval (Figure 20).

DISCUSSION

Relative abundance estimates

The catch reports returned indicating positive identification of white marlin and roundscale spearfish were completed and submitted voluntarily by recreational fishermen. Although the fishermen were provided with a simple morphological guide to distinguish between the two species, the observations are only as good as the care they took to properly evaluate the diagnostic characters. The fishermen who reported their catches operated out of ports ranging from Massachusetts to North Carolina. Fishing was, however, concentrated in the Mid-Atlantic Bight with most boats leaving from Ocean City, MD or Cape May, NJ.

The relative abundance of white marlin and roundscale spearfish revealed from these catch reports was in stark contrast to tournament landings in the Mid-Atlantic Bight for the same years. At the White Marlin Open (WMO) in 2011, five of the 20 putative white marlin brought to the weigh station were roundscale spearfish (25%), and in 2012, three out of eight were roundscale spearfish (38%) (Loose, unpublished). At the 2011 Mid-Atlantic $500,000 tournament (MA500), six out of sixteen were roundscale spearfish (38%), and in 2012 all 14 of the putative white marlin were actually white marlin. There were no roundscale spearfish (Graves and McDowell, unpublished). The mean percentage of roundscale spearfish from the two tournaments in 2011 and 2012 was 25%, which is substantially lower than some past years of the tournaments, but is significantly higher than the 1.8% of

roundscale spearfish from the catch reports, or the 2% from my personal field observations.

The WMO is held annually during the first full week of August, and the MA500 generally follows two weeks later. Tournament regulations for the MA500 and the WMO require fishermen to fish within 125 nautical miles (231.5 km) of the Cape May sea buoy and within 100 nautical miles (185.2 km) of the Ocean City Inlet sea buoy, respectively. It may be possible that higher numbers of roundscale spearfish are present in this small area during this limited time period than they are throughout the entire Mid-Atlantic Bight in the summer and fall. Although this area is well within the range of fishing effort for the fishermen who submitted catch reports, the effort concentrated in this small part of the western North Atlantic during the weeks of the WMO and MA500 is not matched during other times of the year. Another possible reason for this discrepancy in roundscale spearfish catches could be related to size, as fish brought to the weigh stations represent the largest fish caught during the tournaments. It is possible that the there is a higher proportion of large roundscale spearfish present in the Mid-Atlantic Bight during August. Unfortunately, there are no records of estimated sizes of the roundscale spearfish and white marlin released during the tournaments, so the size distributions of the two species remain unknown. Although I requested estimated sizes of the roundscale spearfish and white marlin recorded in the catch reports from cooperating fishermen, the estimates submitted were in very broad categories and not particularly useful for constructing size distributions.

Seasonal movements

Previous tagging studies of white marlin movements have primarily used net displacement as a metric. A study by Prince et al. (2005) estimated displacements of six white marlin tagged for 30 days as 59-496 km, or an average across all six fish of 6.3 km/day. Another study estimated displacements of 30-1170 km for white marlin that were tagged for periods of 5 or 10 days (Horodysky et al. 2007). The fish tagged for five days were estimated to move an average of 14.5 km/day, while the fish with 10-day tags were estimated to move 27.6 km/day. Mather et al. (1972) reported net displacements and times at liberty for four white marlin that were released with conventional tags (between Cape Hatteras, NC, and Cape Cod, MA during the summer months) and subsequently recaptured. These four white marlin had minimum straight line displacement distance rates of 14.2, 15.3, 15.6, and 67.1 km/day. The last rate of 67.1 km/day was for a white marlin that traveled 500 miles, from the coast of North Carolina to Georges Bank (off Cape Cod) in twelve days, where net movement was likely aided by northward-flowing Gulf Stream.

White marlin undertook directed seasonal movements, primarily moving east out of the Mid-Atlantic Bight in September and October past the continental shelf break and the Gulf Stream, before turning south. At this point, most fish made directed southward movements toward the Caribbean, and many toward the Dominican Republic in particular.

Measurements of displacement as the minimum straight line distance traveled likely underestimates the actual distance traveled. Although the speed and distance traveled by white marlin I measured varied throughout the track, the mean daily rates of movement ranged from 39-98 km/day, with an overall mean rate of 65 km/day, or 2.7 km/hr (*SEM*=5.74). This value is considerably larger than the mean values based on minimum straight line distances discussed above. To examine the magnitude of underestimation resulting from the use of minimum straight line distances relative to distances based on geolocation, both values were calculated for the individuals in this study (Table 1). Over all nine marlin, the minimum straight line distances (MSLD) ranged from 2% to 50% of the geolocation distances (mean=24%, *SEM*=5.7), and the roundscale spearfish MSLD was 80% of the geolocation-based distance.

The minimum straight line distances estimated from conventional and electronic tags with shorter deployment times likely have less discrepancy between net displacement and actual distance traveled than tags that remain attached for longer periods. Yet even for short deployments, the underestimate of total distance can be substantial (Table 1). As an example of a shorter term tag, the net displacement of WHM 5 was estimated at 463 km over a period of 40 days. However, geolocation estimates show that this fish traveled 2859 km. In this case, the displacement estimate is only 16% of the geolocation-based distance. For WHM 1, where the PSAT remained attached for 325 days, the distance between the tagging location and the location of tag release was 1292 km. However, the

light-based geolocation analysis suggests that this fish actually traveled over 10820 km. Another example is provided by WHM 2, which had a net displacement of roughly 445 km. Over the period of 365 days, this fish made a complete loop from the Mid-Atlantic Bight, southward to the Brazilian coast, and back to the Mid-Atlantic Bight. It traveled a minimum distance of 22846 km. In this case the displacement distance is only 2% of the geolocation-based distance.

Fishing reports suggest that large numbers of white marlin are present in waters around Hispaniola, and particularly off the eastern coast of the Dominican Republic. Prince et al. (2005) confirmed spawning activity in this area during the spring by sampling for larval billfishes in parallel with tagging of adult billfishes, as well as examining adult ovaries. Of 18 istiophorid larvae captured in neuston tows in April and May of 2003, eight were white marlin, four were blue marlin, and six could not be identified to species. Examination of ovaries from landed white marlin indicated that spawning had likely occurred within the previous 24 hours, and was likely to happen again in the next 12 hours. During this sampling period, seven adult white marlin were released with PSATs attached and tracked for 30 and 40 days. The displacements of these fish ranged from 59-496 km, or 2-13 km/day (mean=6.3 km/day). These distances are considerably shorter than the distances traveled by white marlin in the present study. Prince et al. (2005) suggest that these short displacements represent constrained movements that may be related to spawning activity. However, my data suggest that these fish may not be exhibiting reduced daily movements. Although the fish did spend a greater amount of time within a

restricted geographic area and were not making directed movements, they still maintained relatively high daily displacements.

Fish tagged in the Mid-Atlantic Bight showed a high degree of connectivity with the Caribbean. Five of the seven marlin that were tagged for longer than 40 days spent time in waters around the Dominican Republic, and four of these fish were present in the area of, or traveled through, the Mona Passage. Only one of these fish (WHM 2) had a PSAT attached during the spring spawning season due to tags being deployed in the fall. The fish was, however, present in these waters during the spawning season. The presence of multiple tagged fish in this area, combined with direct evidence of spawning from the Dominican Republic and Mona Passage in the spring and early summer (Prince et al. 2005; Arocha and Bárrios 2009), suggests that movement to this area may be related to spawning. White marlin are common off the Dominican Republic, and the country hosts a thriving white marlin fishery year-round. In 2013, the Dominican Republic was named the number one area for recreational white marlin fishing (http://billfishreport.com/billfish-report/2013). Although the data show that most of the white marlin from my study associated with the Dominican Republic in the fall and winter, the tags from these fish released well before the spring spawning season. It is therefore possible that these fish overwintered in the area and were thus present for spawning during the late spring.

White marlin that left the U.S. Mid Atlantic in the fall exhibited a range of movement, including fish that were tagged close together in time. The existence of

separate contingents within the population is one possible explanation for this observed diversity. Contingents were defined by Clark (1968) as "a group of fish that engage in a common pattern of seasonal migration between feeding areas, wintering areas, and spawning areas". Contingents are not genetically distinct, but are separate groups within one population. It is interesting to note the difference in paths taken by WHM 1 and WHM 2, which were tagged within one month of each other in the same general area of the Mid-Atlantic Bight, but took very different paths. WHM 1 remained along the U.S. Atlantic Coast throughout the fall and winter, moving north and south along the continental shelf in a seemingly haphazard manner, without any clear, directed movements (Figure 3). During this same time, WHM 2 made a directed movement of nearly 5000 km (almost twice the distance covered by WHM 1 in the same amount of time) toward the southeast. It then turned west toward the Caribbean (Figure 4). It has been hypothesized that energy allocation early in life may result in differing migration patterns later in life, in terms of retaining energy, or allowing for exploratory behaviors involving habitat shifts or movements (Secor 1999). Although prey availability or differing oceanographic conditions could play a role in fish movements, it is possible that one of these two white marlin was better equipped energetically to venture greater distances in search of prey, overwintering habitat, or spawning areas.

Overall, my data suggest the importance of regional connectivity between the Mid-Atlantic Bight and the Caribbean, and highlight some of the potential paths white marlin use to travel between these regions. Although only one fish (WHM 2)

completed a circuit and returned to the Mid-Atlantic Bight, it is possible that others would have demonstrated similar movements with longer term tags. Ortiz et al. (2003) noted that conventionally tagged white marlin were often recaptured in the same general location and season after one year or multiple years, a finding that suggests that white marlin undertake cyclical annual movements and possibly exhibit seasonal site fidelity. Although only one individual in my study was tagged for a full 365 days, this single fish supports cyclic movements and site fidelity in white marlin, as WHM 2 returned to the same general area where it had been tagged the previous year.

Habitat utilization

Tagged fish showed habitat utilization consistent with post-release survival. The shortest duration of tag attachment was eight days. Data from this tag suggest that this fish (WHM 8) was preyed upon. WHM 8 had the longest fight time of the fish in my study (27 minutes), was hooked in the corner of the lower jaw, and did not bleed. Alongside the boat, WHM 8 was given a condition score of seven out of ten, and it was resuscitated in the water before being released. After eight days, it is difficult to say whether the capture event had a significant effect on this fish's ability to avoid predators. Studies of post-release survival in white marlin used tags deployed for a minimum of five days, (Horodysky and Graves 2005; Kerstetter and Graves 2006), which suggests that beyond five days mortality cannot be attributed to the capture event.

My data on habitat utilization data, including time at depth and time at temperature, were generally consistent with those of previous studies of white marlin tagged for shorter durations. However, there was considerable variation evident between individuals within geographic regions, as well as differences between geographic locations. Horodysky et al. (2007) tagged 20 white marlin along the U.S. East Coast for periods of 5 or 10 days, eight in the Northern Caribbean for 5 or 10 days, and 19 off of Venezuela for 10 days. Their results indicated that temperature and depth habitat utilization varied by region, with white marlin tagged off the U.S. East Coast spending the largest amount of time in the upper 10 m of the water column, while those tagged in the northern Caribbean and offshore of Venezuela spent less time in surface waters of 0-10 m. I found similar results with white marlin spending less time in surface waters in the Caribbean than fish along the U.S. East Coast.

All white marlin, as well as the roundscale spearfish in the North Atlantic, spent a great majority of their time in the 0-100 m stratum throughout their tracks. Horodysky et al. (2007) found that white marlin tagged in the northern Caribbean and off Venezuela spent a greater percentage of their total time at depths of 20-30 m (and in cooler temperatures) than at depths of 10-20 m. Similar results were found for some time periods in the present study. Over the five segments examined for WHM 2, this pattern was more pronounced in the Caribbean Sea and during the time the fish was travelling between the Caribbean and the Mid-Atlantic Bight, than it was when the fish was along the U.S. East Coast in September or while

it remained in the same general area far offshore from mid-December to mid-April. However, in the fall and through mid-December, when WHM 2 left the Mid-Atlantic Bight and was moving offshore, the time spent between 10-20 m, and 20-30 m was nearly equal. Brill and Lutcavage (2001) assert that yellowfin tuna are physiologically limited by the change in water temperature, as heart rate (and therefore cardiac output) decreases with decreasing water temperature, which limits aerobic performance. It has been suggested that billfish may react similarly to cold water, and therefore, try to avoid it for prolonged periods (Brill et al. 1998; 1999; Brill and Lutcavage 2001). Horodysky et al. (2007) suggested that the tendency of marlin to spend more time in slightly deeper waters of 20-30 m than in the 10-20 m stratum may be a compromise between the physiological need to remain in warm waters to maintain cardiac function, while also needing to remain in deeper, cooler waters to search for prey.

In addition to spending the majority of their time in warm surface waters, white marlin spent 98% of their time within eight degrees of the SST. Similar results have been reported for other istiophorid species, including blue marlin (Holland et al. 1990), striped marlin (Holts and Bedford 1990; Brill et al. 1993), and black marlin (Pepperell and Davis 1999). This is most likely due to the physiological limitations mentioned above, as it has been suggested that yellowfin tuna will remain within an eight degree range of the sea surface temperature, rather than seeking out any particular temperature (Brill et al. 1998 and 1999; Brill and Lutcavage 2001).

White marlin tagged off the Dominican Republic in April and May by Prince et al. (2005) experienced temperatures ranging from 16.8-30.0˚C, and depths of 0-368 m over the 30-40 day period their PSATs remained attached. In my study, data pooled for the time white marlin spent in the vicinity of the Dominican Republic, showed they experienced water temperatures of 18-30˚C. In addition to fish being present in this area in the fall, winter, and spring months, some individuals were also present in the Caribbean in summer months, when water temperatures are warmer. The maximum depth reached by a white marlin in this location in my study (210 m) was considerably less than the 368 m reported Prince et al. (2005). However my data show excursions to such depths to be rare events, and the overall mean depth for this location was only 32 m (*SEM*=0.2).

Hoolihan et al. (2012) examined data from 14 white marlin tagged during September in the western North Atlantic. Tag attachment durations ranged from 6 to 150 days (mean 92 days). Over this period of time, the fish experienced temperatures ranging from 8-30˚C and depths of 0-304 m. My data show that white marlin in the northwest Atlantic experience a narrower range of depth and temperatures, with depths ranging from 0-220 m, and temperatures of 12-31˚C.

Longer term PSAT attachments allowed for examination of the same individual across different areas. The habitat utilization of WHM 1, over three separate periods of time and geographic areas showed similar percentages of time spent at depth, although the time spent in surface waters decreased slightly as it moved east throughout its track, and more time was spent at depths greater than

100 m during its directed movement away from the U.S. East Coast. This fish spent more time at cooler temperatures along the U.S. East Coast than in the other areas, but this appears to be due to cooler water temperatures throughout the water column since the fish spent more time in the top 10 m in this area than in other regions. The mean temperatures across segments were within the range of 22-23˚C. WHM 2 exhibited similar time at depth profiles throughout the first three segments of time at liberty and geographic areas. Among these first three segments, the mean time spent at 0-10 m was 50% (*SEM*=2), the mean for 0-100 m was 97% (*SEM*=0.9), and the mean time at depths greater than 100 m was 1.4% (*SEM*=0.9). As the depth profiles remained similar, the trend of occupying warmer temperatures reflects the general increase in water temperatures as the fish move south. During the last two segments, however, the habitat utilization of this fish changed. While in waters around the Caribbean Islands, the time in the upper 10 m of the water column halved (28%), and much more time was spent at depths greater than 100 m (19%). Consistent with warmer water temperatures present in the Caribbean, those experienced by WHM 2 in this segment were warmer, with only 3% of time spent at 20-24˚C. During this time, WHM 2 passed through the known spawning area east of the Dominican Republic (Prince et al. 2005; Arocha and Bárrios 2009).

During my study, only two white marlin had PSATs attached during the late spring/early summer months, when spawning has been confirmed. WHM 2 was in the spawning area off the Dominican Republic during June. Additionally, white marlin spawning has been observed in Bermuda waters during summer months

(Heppell, unpublished), and blue marlin spawning has been observed near Bermuda in July (Luckhurst et al. 2006). I examined habitat utilization of WHM 1 during the time spent east of Bermuda in potential spawning grounds, as well as for WHM 2 during the time it spent in the Dominican Republic spawning area. Time at depth and time at temperature records during these time periods for these two fish were found to be quite different (Tables 3 and 4). Speeds for movements of both fish were also considered while in potential spawning habitats, and these differed as well. WHM 1 averaged 23 km/day (1.0 km/hr) while in potential spawning grounds off Bermuda, and WHM 2 averaged 74.0 km/hr (3.1 km/hr) while passing through the spawning grounds of the Dominican Republic. However, little is known about white marlin habitat utilization and movements in spawning areas (Mather et al. 1972; Prince et al. 2005), and it is not possible to know whether differences observed for these fish were related to spawning. Oceanic conditions vary between these two locations and would likely result in differences in habitat utilization.

Previous studies indicate a multidirectional pattern of displacements of blue marlin and white marlin near the Dominican Republic (Prince et al. 2005), and of blue marlin near Bermuda (Graves et al. 2002). I observed multidirectional movements in several individuals as they covered great distances while remaining within relatively small areas around the Dominican Republic and off the northern and northeastern coasts of South America. This was also seen as individuals took slightly different tracks around the Caribbean Islands. In the last segment of the track of WHM 2, as the fish was returning to the Mid-Atlantic Bight from the

Caribbean, it spent 99% of its time in the upper 100 m, and the time at 0-10 m (29%) was similar to the Caribbean Sea segment. Water temperatures experienced in this region were divided nearly equally, with 44% spent at 20-24°C and 45% spent at 24-28°C.

Previous tagging studies of istiophorid billfishes have reached different conclusions regarding diel differences in habitat utilization. Earlier acoustic studies showed diel differences in blue marlin (Holland et al. 1990; Block 1992) and black marlin (Pepperell and Davis 1999) habitat utilization, but not in striped marlin (Brill et al. 1993). More recent PSAT studies have reported diel differences in black marlin (Gunn et al. 2003) and blue marlin (Kerstetter et al. 2003; Goodyear et al. 2008) habitat utilization, while others reported differences for some individuals (Graves et al. 2002), or some geographical regions, but not others (Kraus and Rooker 2007). In one study of white marlin, diel trends were observed qualitatively in some areas of the tracks of some individuals, but these differences did not persist throughout the length of the tracks (Horodysky et al. 2007). Studies that have shown diel differences in habitat utilization suggest that the fish generally spend time in deeper, cooler waters during the daylight hours and shallower, warmer surface waters at night. In the present study, pooled diel data for means of daytime and nighttime hours showed significant differences in depth and temperature distributions, with white marlin experiencing cooler and deeper waters during the day than at night. Although current PSAT technology cannot collect data on prey availability or feeding, Kraus and Rooker (2007) found that diel patterns of vertical movements correspond

to the lunar phase, resulting in increased nighttime vertical excursion activity during the full moon. The suggestion of visual sight feeding in low light conditions, such as at depth during the day, or at night during a full moon, is supported by the specially adapted vision present in billfish that allows foraging at low light levels (Block and Finnerty 1994; Fritsches et al. 2003; Fritsches et al. 2005).

CONCLUSIONS AND FUTURE WORK

This study is the first to report on long-term (up to one year) PSAT deployments on white marlin and to incorporate geolocation analyses for this species. My results provide insights into white marlin seasonal movements and habitat utilization (for up to one full year), and suggest possible seasonal site fidelity. Additionally, my results illustrate connectivity of white marlin throughout the western North Atlantic, especially between white marlin from the U.S. Mid-Atlantic Bight and the Caribbean Sea.

My project began as a comparative investigation of white marlin and roundscale spearfish movements and habitat utilization, and was subsequently modified to focus solely on white marlin due to the scarcity of roundscale spearfish encountered in the recreational fishery. Modifying the project at the end of August 2012 resulted in fish that were tagged over a period of two fall field seasons, which resulted in tag information that was heavily weighted for observations in the fall and winter months. Clearly additional studies of "Mid-Atlantic" white marlin tagged during the spring and summer months are needed.

There are inherent challenges involved in working with PSATs. A major problem for studies of highly migratory species has been the premature release of tags which has been attributed to a variety of factors including poor attachment, tag fouling, infection at the puncture site, or predation of the tag and/or fish. Also possible are lower percentages of data transmission, and in some cases, complete

tag failure. All of these tend to reduce the size of the data set or the sample size overall. Considering the high costs of PSATs, any research to develop methods to increase tag retention would greatly benefit our understanding of the animal's movements (Musyl et al. 2011).

My study focused on white marlin caught in a very limited area over a short period of time, and thus the results may not be completely representative of white marlin from the western North Atlantic or the species as a whole. Future studies should focus on concentrations of white marlin in other areas and times. My results suggest that directing tagging efforts on white marlin in the Caribbean Sea, especially during winter months, could provide critical information on connectivity and mixing within the western North Atlantic.

Additionally, future work should aim to provide more information regarding spawning sites in the western North Atlantic, including waters around the Dominican Republic and Bermuda, as well as individual fidelity to known spawning locations over multiple years. The deployment of more long term tags could help to elucidate the possibility of a mixed stock assemblage in the U.S. Mid-Atlantic Bight, as well as investigate directed seasonal movement patterns. These data could potentially be useful to establish international management measures for white marlin to ensure that they are protected throughout their range.

This study also raises many questions about roundscale spearfish. Information is lacking regarding their movements and spawning areas, and the one fish tagged in this study provides the first, albeit limited, information on seasonal

movements and habitat utilization. Future PSAT research is needed on roundscale spearfish, but based on my experience, it will likely require considerable time, perseverance, and a group of fishermen dedicated to finding these elusive fish.

CHAPTER 2
TABLES AND FIGURES

Table 1: Tag deployment information for roundscale spearfish (SPG) and white marlin (WHM) tagged with PSATs in the Mid-Atlantic Bight in August and September of 2011 and September of 2012, including geolocation based estimates of distance traveled and displacement, or minimum straight line distance (MSLD), for each fish.

				Tagging location		Tag release location		Geolocation	
Fish species and #	Deployment date	Release date	Days at liberty	Latitude (N)	Longitude (W)	Latitude (N)	Longitude (W)	estimate (km)	MSLD (km)
SPG 1	9/10/2011	10/14/2011	34	38.692	73.089	37.903	58.106	1636	1317
WHM 1	8/13/2011	7/1/2012	323	37.085	74.62	32.953	61.346	10820	1327
WHM 2	9/11/2011	9/11/2012	365	37.223	74.706	39.298	69.87	22846	445
WHM 3	9/1/2012	12/26/2012	117	36.998	74.649	22.032	73.143	4444	1846
WHM 4	9/1/2012	3/1/2013	180	36.998	74.649	13.502	74.047	13603	2724
WHM 5	9/1/2012	10/8/2012	40	37.002	74.652	33.525	73.743	2859	463
WHM 7	9/2/2012	10/31/2012	58	36.975	74.636	18.746	77.122	4453	2219
WHM 8	9/2/2012	9/10/2012	8	36.969	74.624	37.416	72.751	835	374
WHM 9	9/7/2012	3/7/2013	180	37.067	74.698	16.444	75.77	11381	2415
WHM 11	9/16/2012	12/28/2012	103	36.336	74.804	33.927	75.845	5099	824

Table 2: Species, identification number, reason for tag transmission, and data recovery rate for pop-up satellite archival tags deployed in this study.

Fish species and number	Reason for tag data transmission	% data received
SPG 1	constant pressure	100
WHM 1	exceeded max depth	88
WHM 2	reached programmed date	87
WHM 3	constant pressure	87
WHM 4	reached programmed date	87
WHM 5	constant pressure	99
WHM 6	did not report	N/A
WHM 7	constant pressure	97
WHM 8	constant pressure	100
WHM 9	reached programmed date	89
WHM 10	did not report	N/A
WHM 11	constant pressure	84

Table 3: Percentage of time at depth and time at temperature, as well as depth and temperature summary data for the entire track of WHM 1 (August 13, 2011-July 1, 2012), and for each of three segments of the track, separated according to time and location. (1) August 13-May 11, the fish remained along the U.S. East Coast throughout the fall, winter, and early spring, and did not make any apparent directed movements. (2) May 11-June 8, the fish made a directed movement nearly due east. (3) June 8-July 1, the fish spent just over one month in the same general area, north of Bermuda.

	Depth						Temperature				
	Time at depth (%)			Depth summary (m)			Time at temp (%)		Temperature summary (˚C)		
Area	0-10 m	0-100 m	100+ m	Minimum	Maximum	Mean (*SE*)	20-24˚C	24-28˚C	Minimum	Maximum	Mean
Entire track	**61.7**	**97.8**	**2.2**	**0.0**	**204.4**	**15.6**	**70.0**	**25.1**	**12.3**	**27.5**	**22.8**
1	62.5	97.9	2.1	0.0	204.4	14.9	68.7	26.7	12.3	27.5	22.8
2	55.1	96.0	3.4	0.0	182.9	25.4	81.8	7.2	19.1	25.8	21.7
3	49.8	98.3	1.7	0.0	139.9	22.0	80.3	18.2	19.6	25.0	22.9

Table 4: Percentage of time at depth and time at temperature, as well as depth and temperature summary data for the entire track of WHM 2, and for each of five segments of the track, separated according to time and location. (1) September 11-September 25, in the Mid-Atlantic Bight. (2) September 26-December 18, the fish left the Mid-Atlantic Bight and made a directed movement to the southeast. (3) December 19-April 15, the fish was not making any apparent directed movements, and was off of northern Brazil. (4) May 18-June 22, the fish was traveling through the Caribbean Sea. (5) June 22-July 15, the fish was making a directed movement from the Caribbean back toward the Mid-Atlantic Bight.

	Depth						Temperature				
	Time at depth (%)			Depth summary (m)			Time at temp (%)		Temperature summary (˚C)		
Area	0-10 m	0-100 m	100+ m	Minimum	Maximum	Mean	20-24˚C	24-28˚C	Minimum	Maximum	Mean
Entire track	**46.7**	**96.5**	**3.5**	**0.0**	**204.4**	**32.7**	**4.5**	**62.6**	**16.7**	**29.7**	**26.3**
1	50.1	98.1	1.9	0.0	118.3	33.3	21.5	70.6	16.7	28.8	25.4
2	47.0	95.0	1.0	0.0	182.9	39.0	10.6	86.6	20.1	28.6	26.1
3	54.0	98.8	1.2	0.0	172.1	26.8	0.8	99.1	19.2	28.0	26.6
4	28.2	81.4	18.6	0.0	204.4	50.4	3.2	79.8	21.2	29.1	26.8
5	29.2	99.0	1.1	0.0	156.0	44.3	43.8	44.7	20.4	29.7	24.9

Figure 1: Light-based geolocation estimates for the tracks of all white marlin. Each color represents the movements of a different fish. Total distances traveled by each fish are presented in the legend.

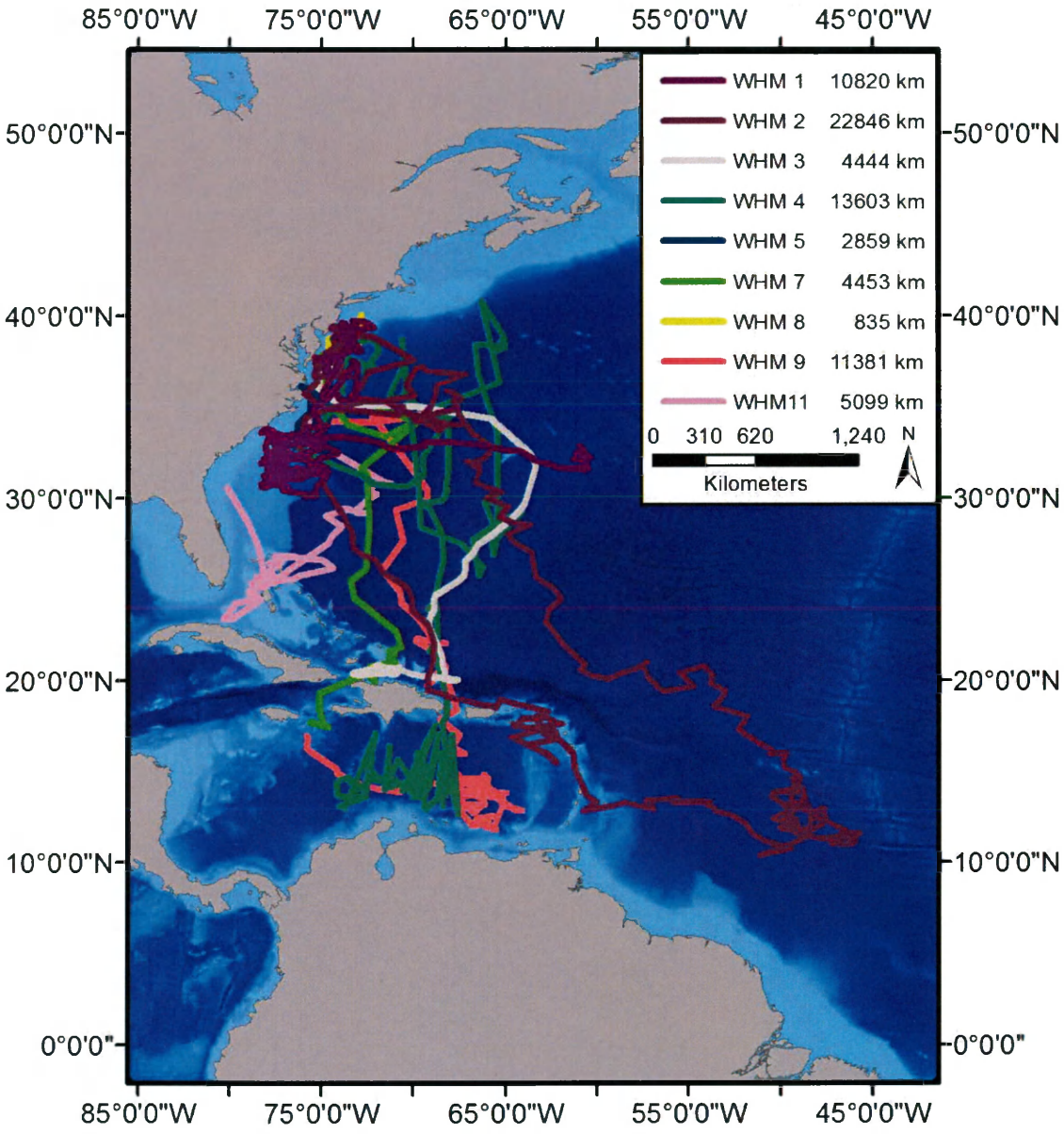

85°0'0"W
75°0'0"W
65°0'0"W
55°0'0"W
45°0'0"W
50°0'0"N
40°0'0"N
30°0'0"N
20°0'0"N
10°0'0"N
0°0'0"
WHM 1 10820 km
WHM 2 22846 km
WHM 3 4444 km
WHM 4 13603 km
WHM 5 2859 km
WHM 7 4453 km
WHM 8 835 km
WHM 9 11381 km
WHM11 5099 km
0 310 620 1,240
Kilometers
N

Figure 2: Light-based geolocation estimates for the tracks of all white marlin combined, with colors indicating the month for each position as noted in the legend.

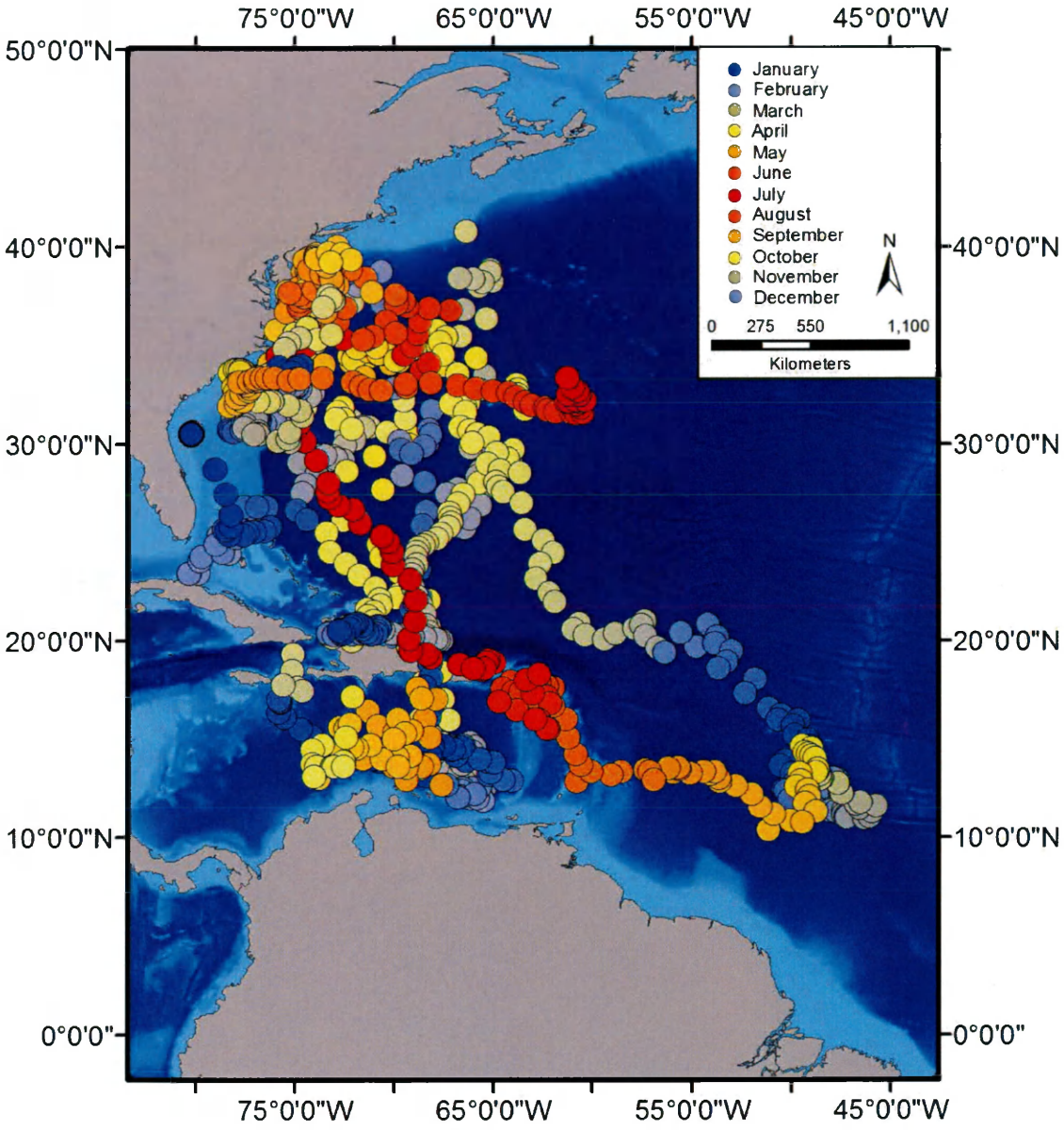
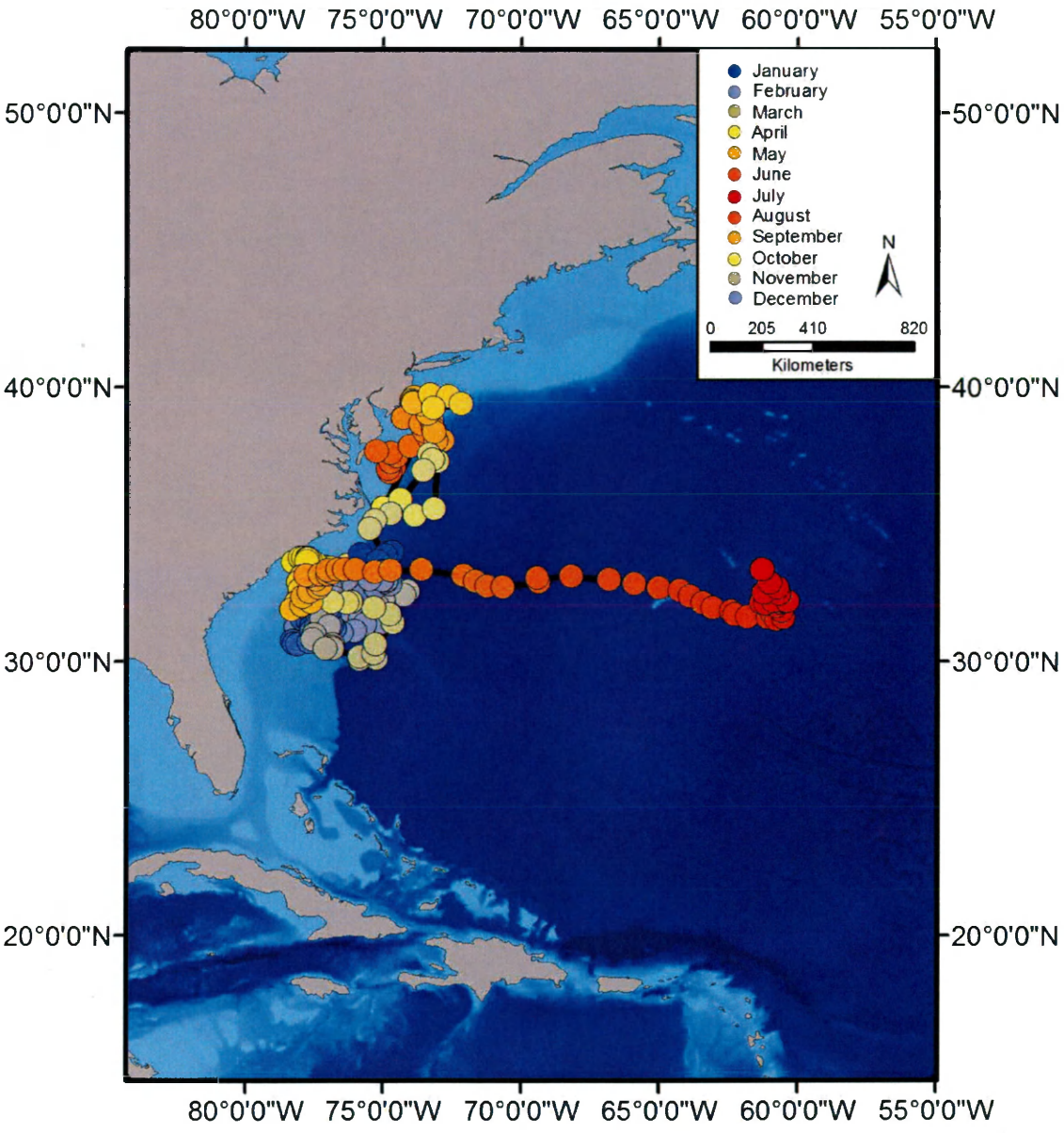

75°0'0"W
65°0'0"W
55°0'0"W
45°0'0"W
50°0'0"N
40°0'0"N
30°0'0"N
20°0'0"N
10°0'0"N
0°0'0"
January
February
March
April
May
June
July
August
September
October
November
December
N
0 275 550 1,100
Kilometers

Figure 3: Light-based geolocation estimates for the track of WHM 1. Tagged for 325 days from August 13, 2011, to July 1, 2012, this fish traveled an estimated 10820 km.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75°0'0"W
70°0'0"W
65°0'0"W
60°0'0"W
55°0'0"W
50°0'0"N
40°0'0"N
30°0'0"N
20°0'0"N
January
February
March
April
May
June
July
August
September
October
November
December
N
0
205
410
820
Kilometers

Figure 4: Light-based geolocation estimates for the track of WHM 2. Tagged for 365 days from September 11, 2011 to September 11, 2012, this fish traveled an estimated 22846 km.

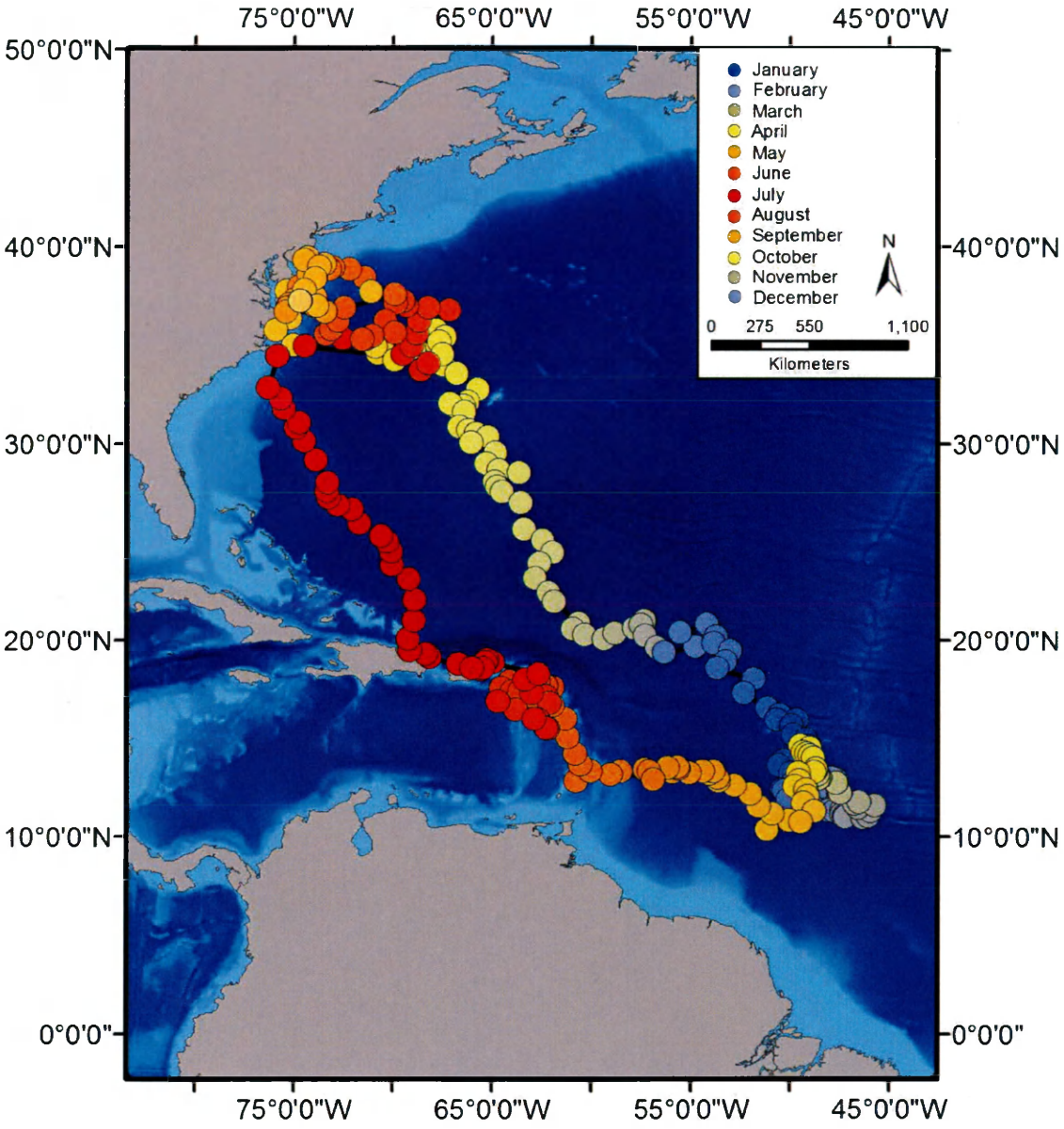

75°0'0"W
65°0'0"W
55°0'0"W
45°0'0"W
50°0'0"N
40°0'0"N
30°0'0"N
20°0'0"N
10°0'0"N
0°0'0"
January
February
March
April
May
June
July
August
September
October
November
December
N
0 275 550 1,100
Kilometers

Figure 5: Light-based geolocation estimates for the track of WHM 3. Tagged for 117 days from September 1, 2012 to December 26, 2012, this fish traveled an estimated 4444 km.

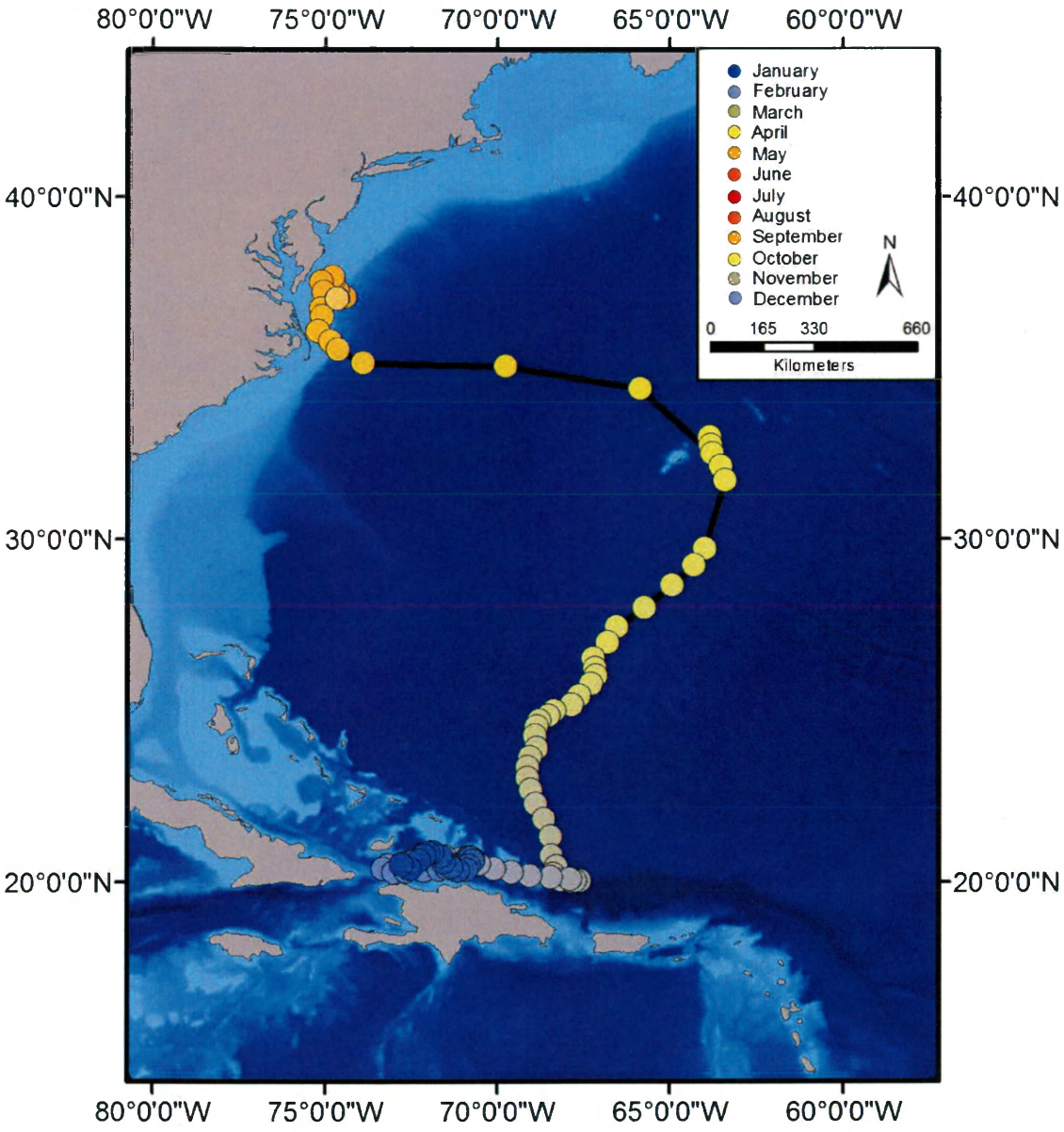

80°0'0"W
75°0'0"W
70°0'0"W
65°0'0"W
60°0'0"W
40°0'0"N
30°0'0"N
20°0'0"N
January
February
March
April
May
June
July
August
September
October
November
December
N
0
165
330
660
Kilometers

Figure 6: Light-based geolocation estimates for the track of WHM 4. Tagged for 180 days from September 1, 2012 to March 1, 2013, this fish traveled an estimated 13603 km.

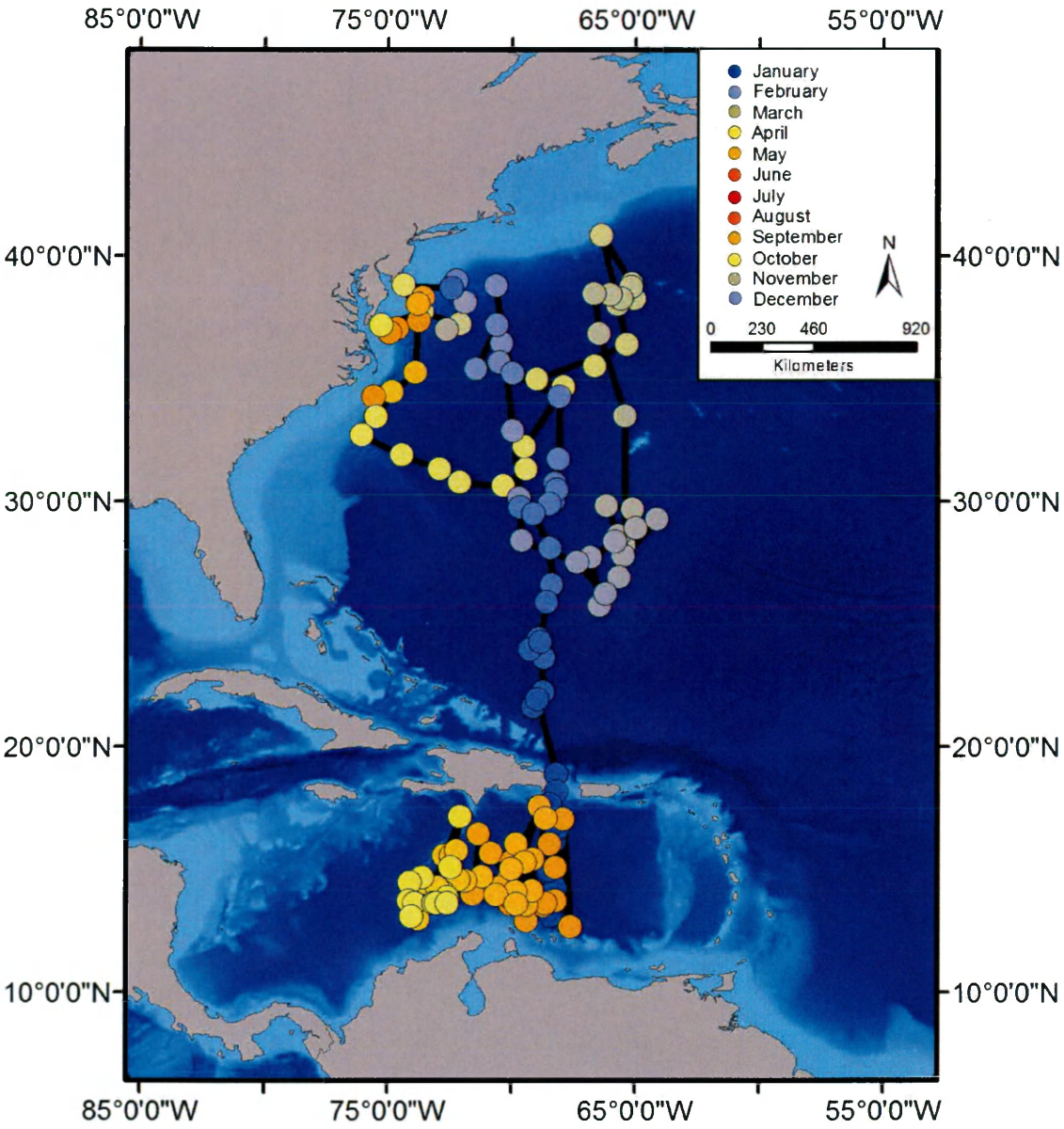

85°0'0"W
75°0'0"W
65°0'0"W
55°0'0"W
40°0'0"N
30°0'0"N
20°0'0"N
10°0'0"N
January
February
March
April
May
June
July
August
September
October
November
December
N
0
230
460
920
Kilometers

Figure 7: Light-based geolocation estimates for the track of WHM 5. Tagged for 40 days from September 1, 2012 to October 8, 2012, this fish traveled an estimated 2859 km.

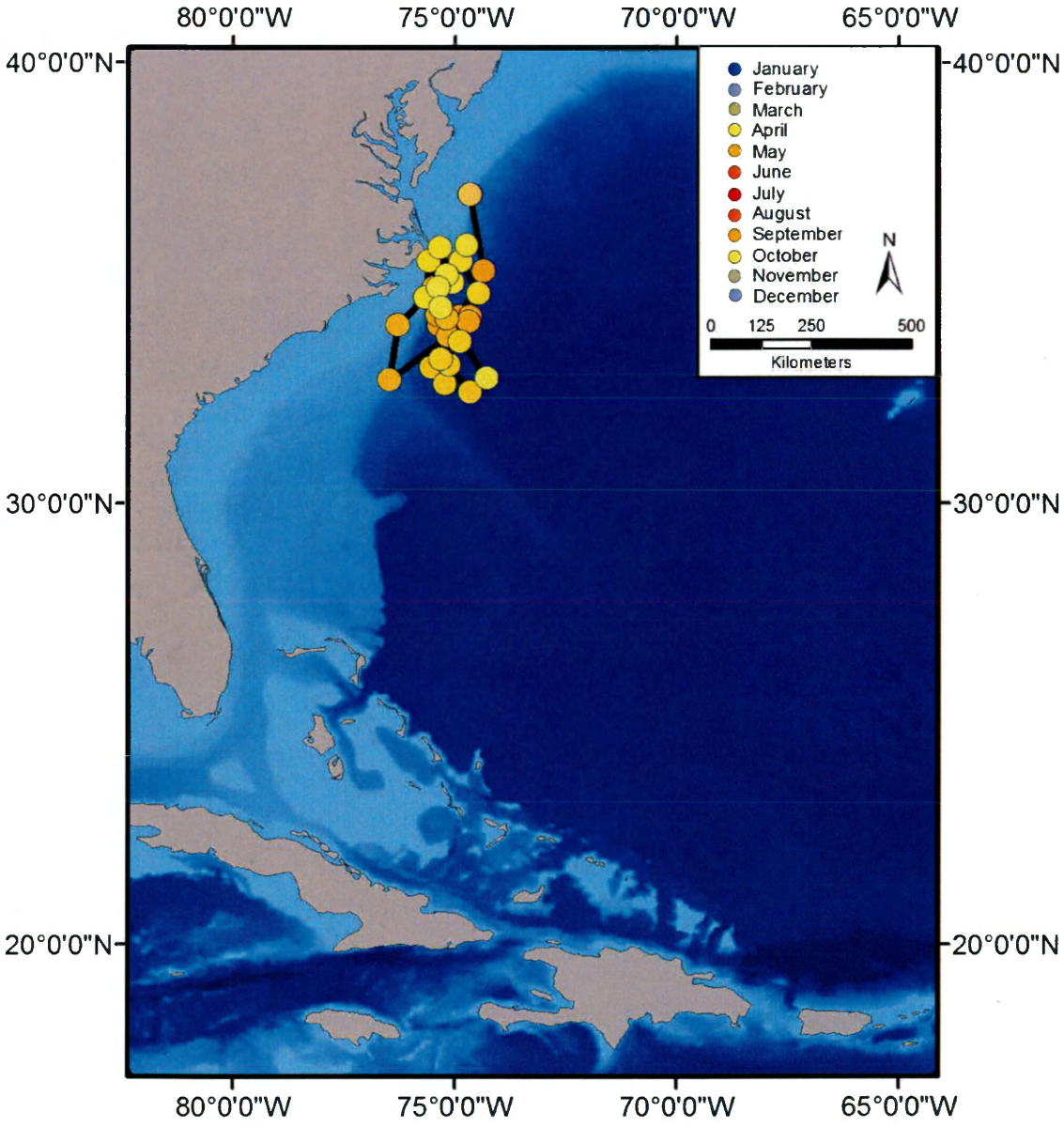

80°0'0"W
75°0'0"W
70°0'0"W
65°0'0"W
40°0'0"N
30°0'0"N
20°0'0"N
January
February
March
April
May
June
July
August
September
October
November
December
N
0
125
250
500
Kilometers

Figure 8: Light-based geolocation estimates for the track of WHM 7. Tagged for 58 days from September 2, 2012 to October 31, 2012, this fish traveled an estimated 4453 km.

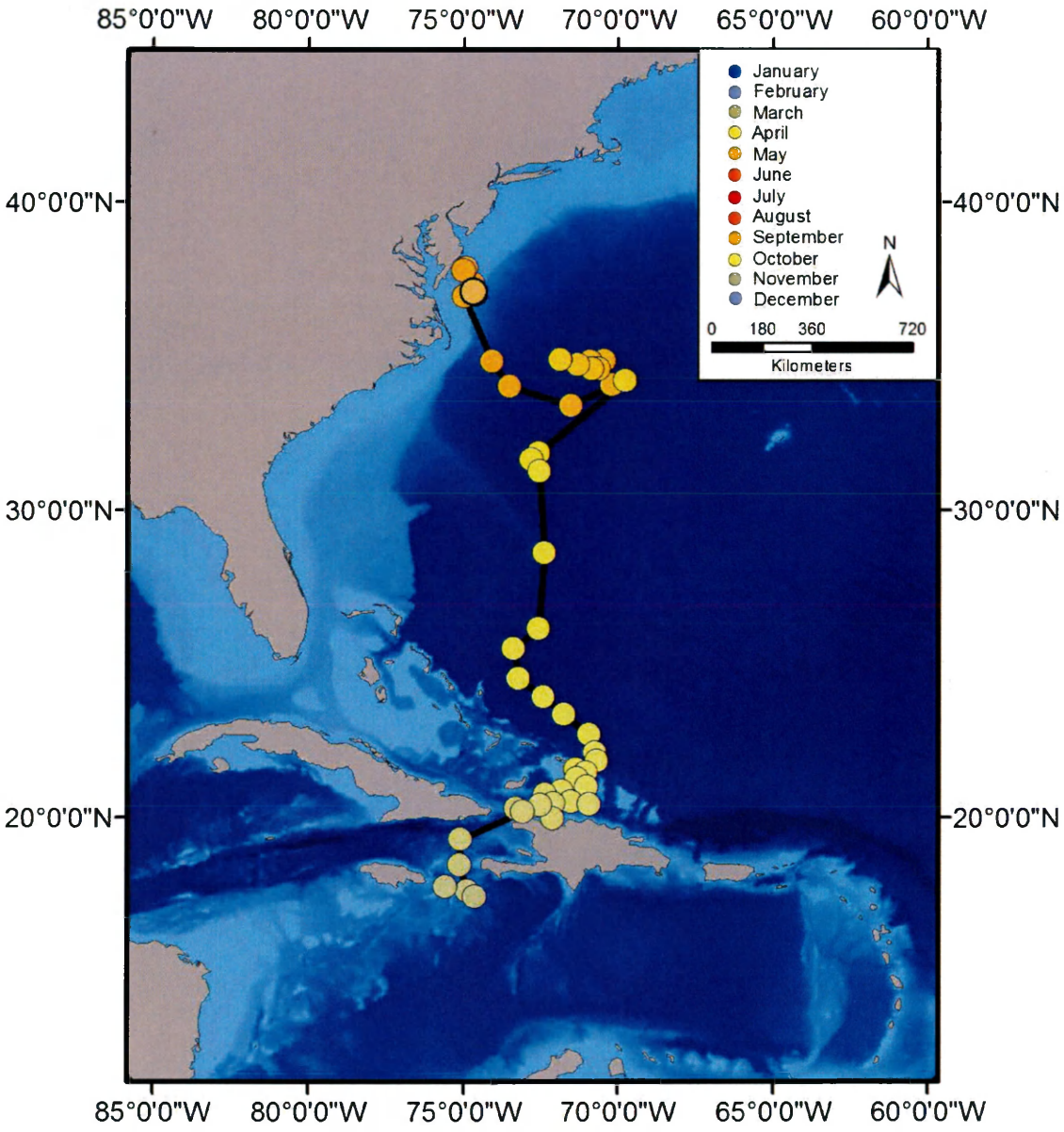

85°0'0"W
80°0'0"W
75°0'0"W
70°0'0"W
65°0'0"W
60°0'0"W
40°0'0"N
30°0'0"N
20°0'0"N
January
February
March
April
May
June
July
August
September
October
November
December
N
0
180
360
720
Kilometers

Figure 9: Light-based geolocation estimates for the track of WHM 8. Tagged for 8 days from September 2, 2012 to September 10, 2012, this fish traveled an estimated 835 km.

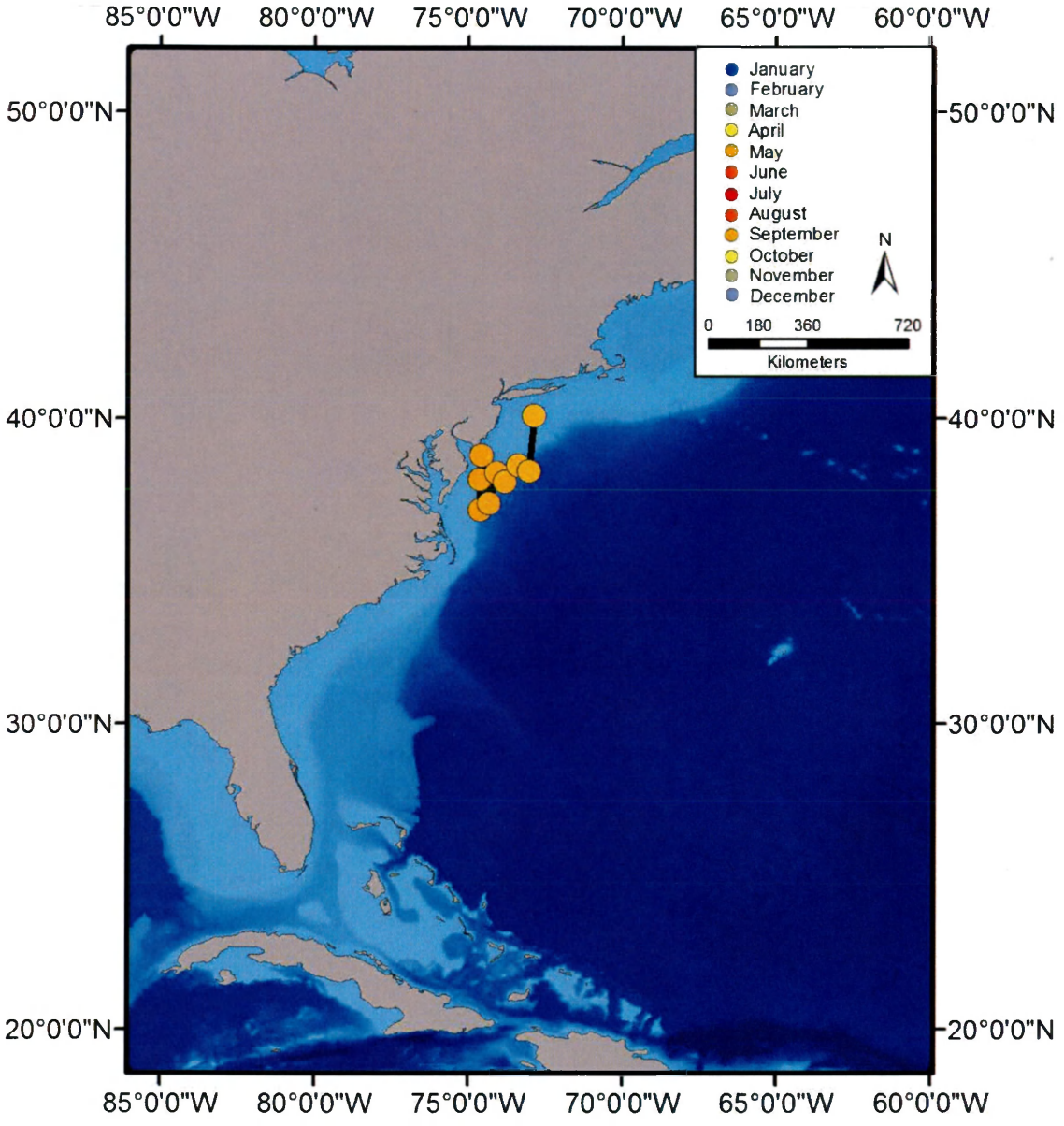
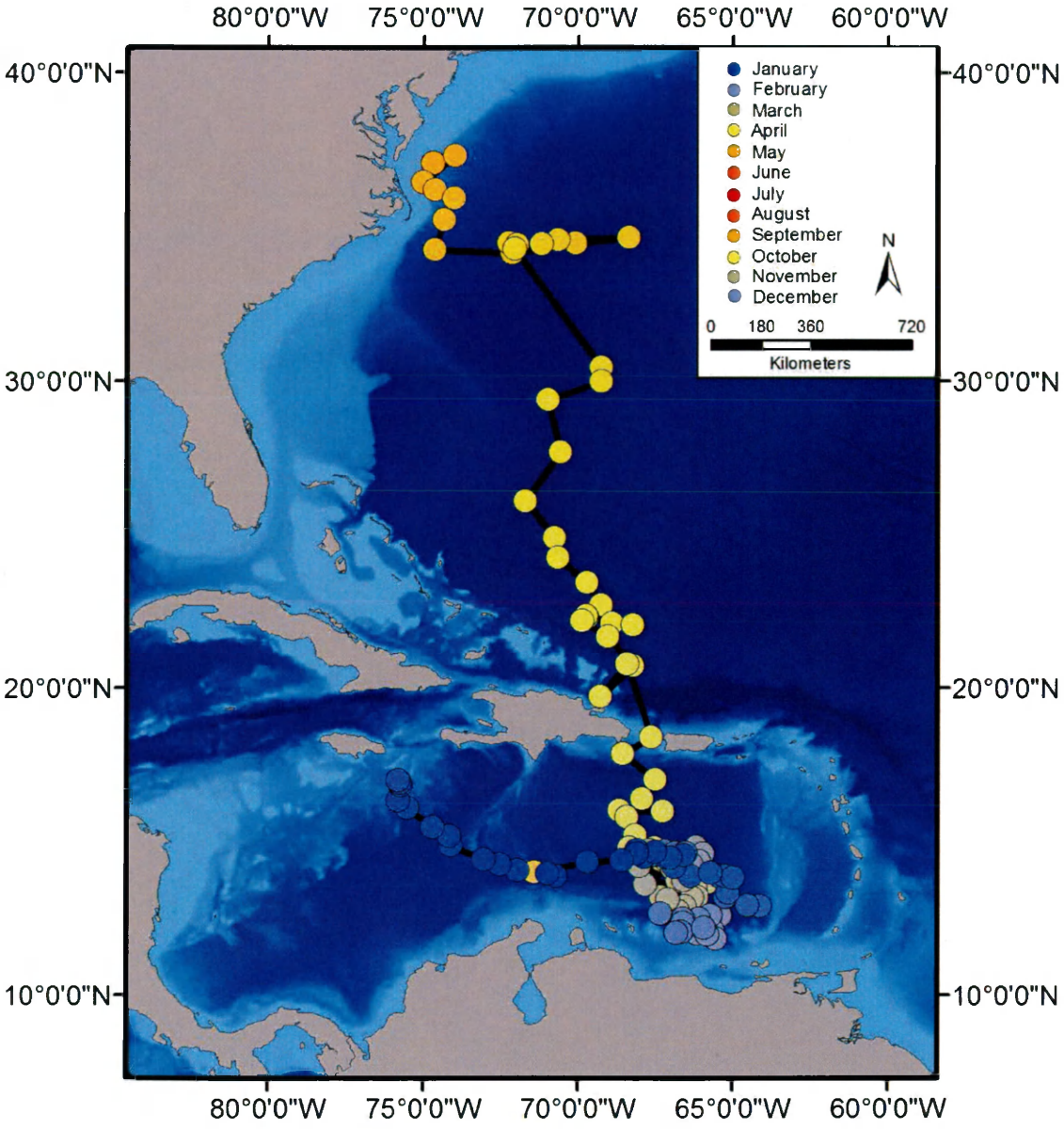

85°0'0"W
80°0'0"W
75°0'0"W
70°0'0"W
65°0'0"W
60°0'0"W
50°0'0"N
40°0'0"N
30°0'0"N
20°0'0"N
January
February
March
April
May
June
July
August
September
October
November
December
N
0 180 360 720
Kilometers

Figure 10: Light-based geolocation estimates for the track of WHM 9. Tagged for 180 days from September 7, 2012 to March 7, 2013, this fish traveled an estimated 11381 km.


80°0'0"W
75°0'0"W
70°0'0"W
65°0'0"W
60°0'0"W
40°0'0"N
30°0'0"N
20°0'0"N
10°0'0"N
January
February
March
April
May
June
July
August
September
October
November
December
N
0
180
360
720
Kilometers

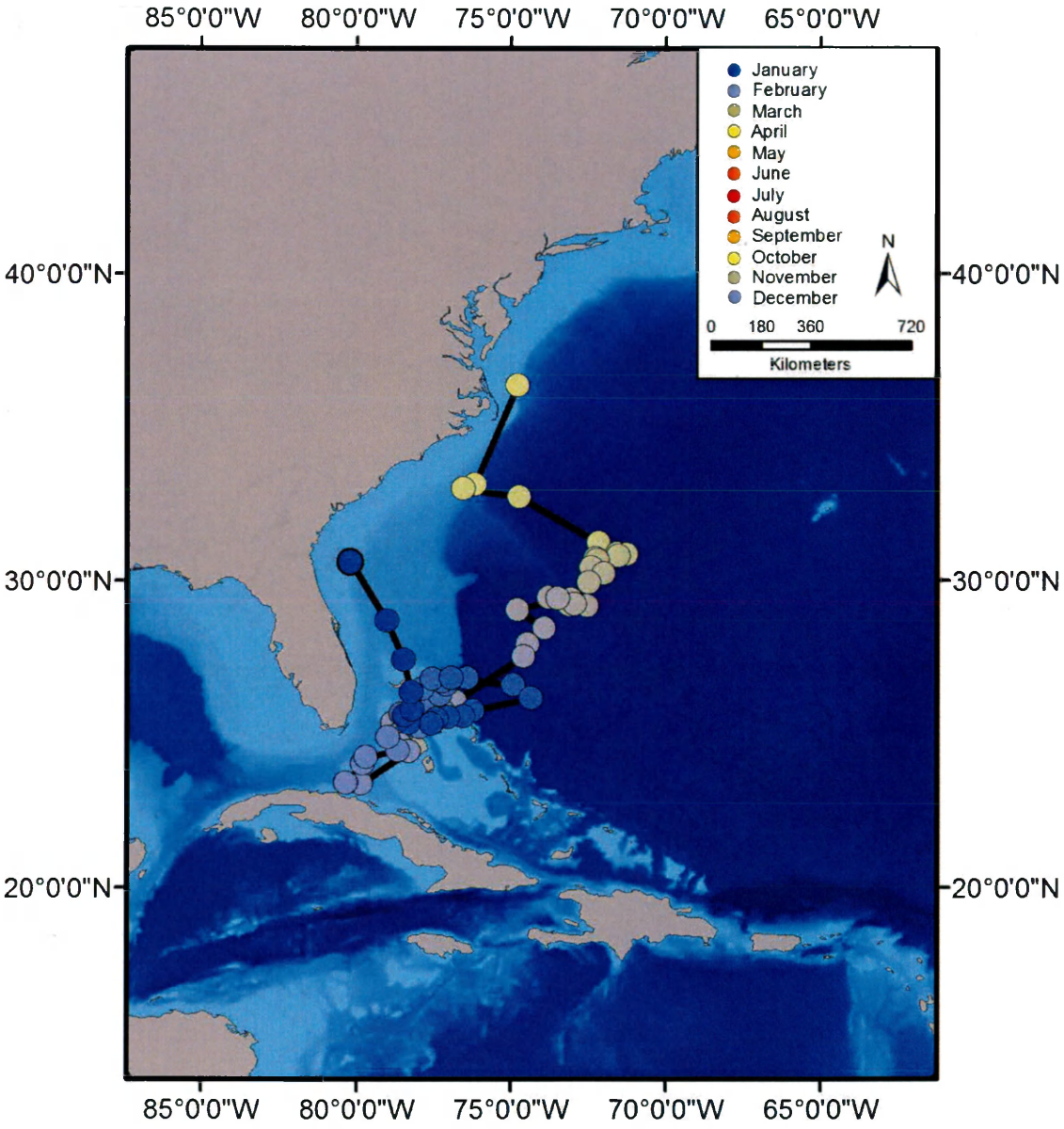
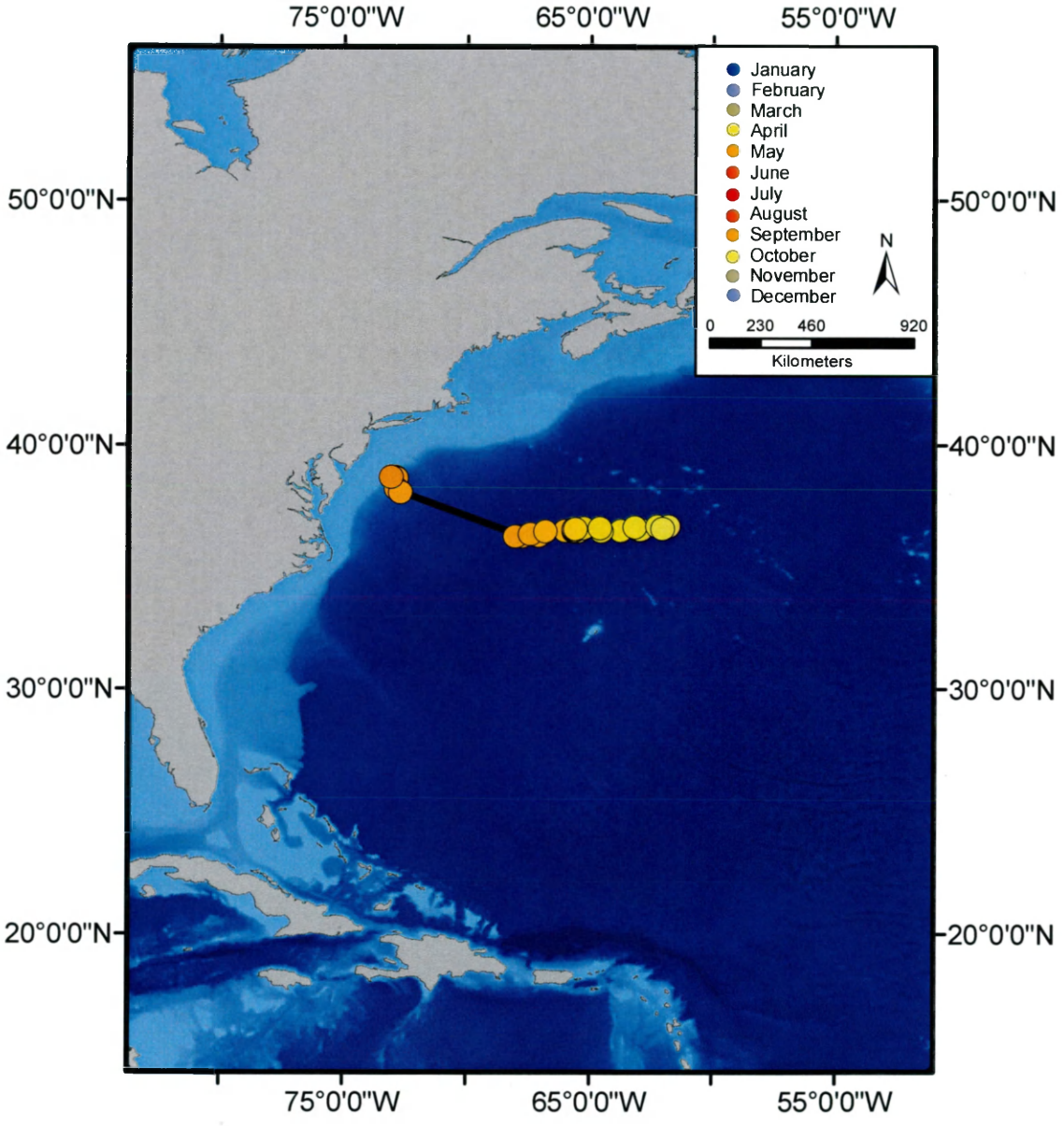

85°0'0"W
80°0'0"W
75°0'0"W
70°0'0"W
65°0'0"W
40°0'0"N
30°0'0"N
20°0'0"N
January
February
March
April
May
June
July
August
September
October
November
December
N
0
180
360
720
Kilometers

Figure 12: Light-based geolocation estimates for the track of SPG 1. Tagged for 34 days from September 10, 2011 to October 14, 2011, this fish traveled an estimated 1636 km.


75°0'0"W
65°0'0"W
55°0'0"W
50°0'0"N
40°0'0"N
30°0'0"N
20°0'0"N
January
February
March
April
May
June
July
August
September
October
November
December
N
0 230 460 920
Kilometers

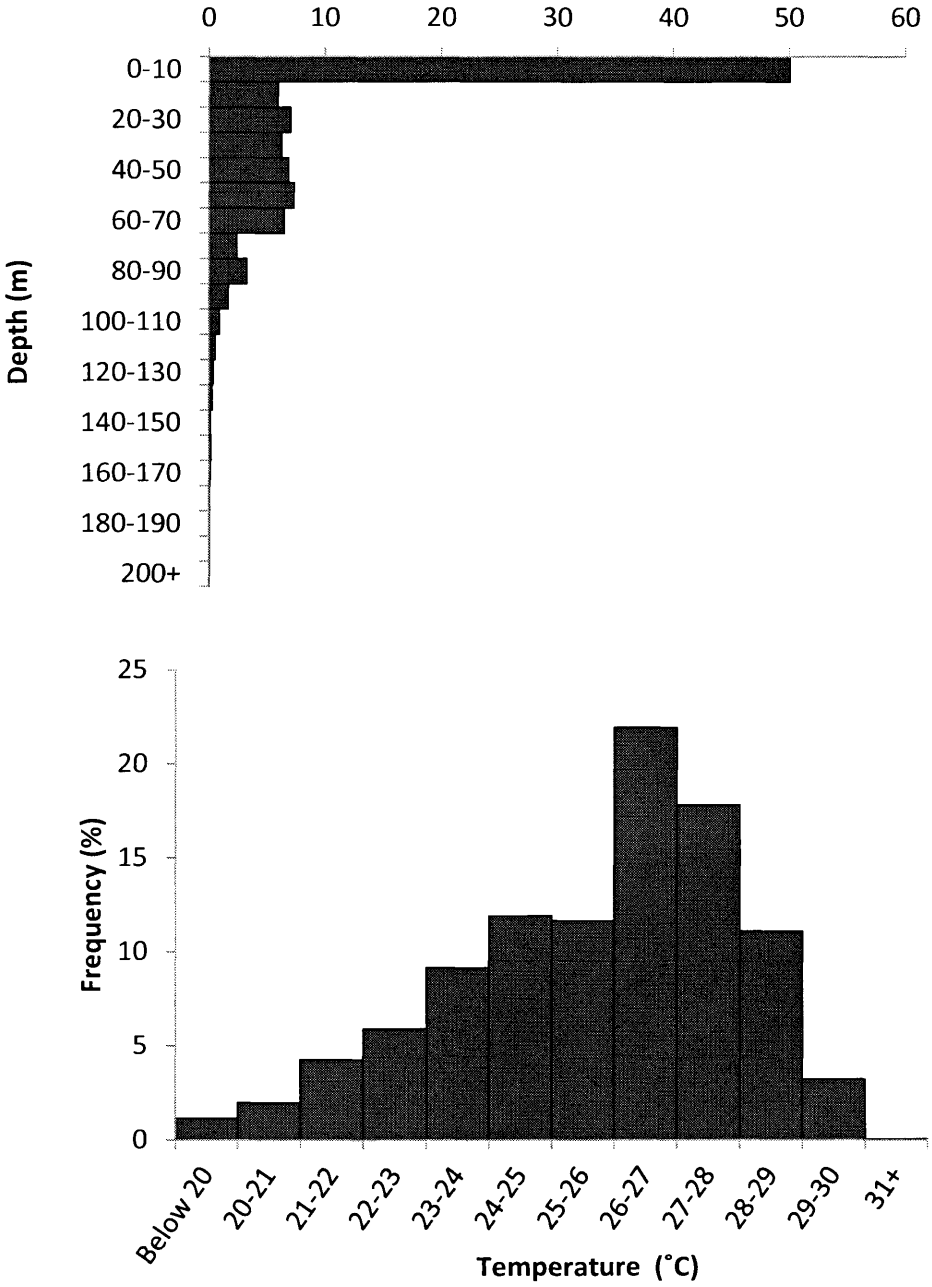


Figure 13: Percent of total time at depth and time at temperature for all white marlin combined.

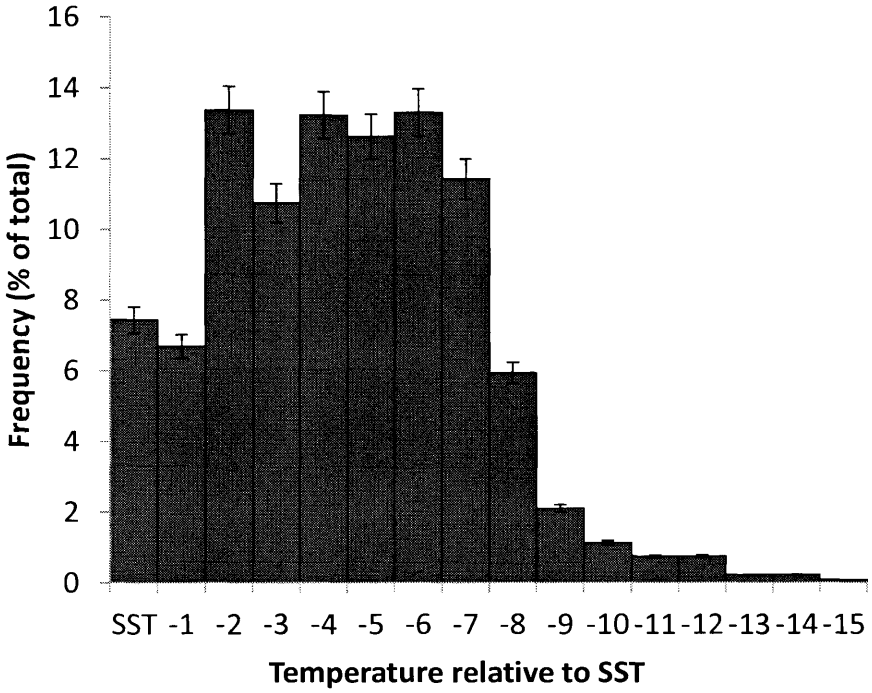


Figure 14: Distribution of maximum daily temperature ranges experienced by the fish relative to SST (the maximum daily temperature) for all white marlin combined.

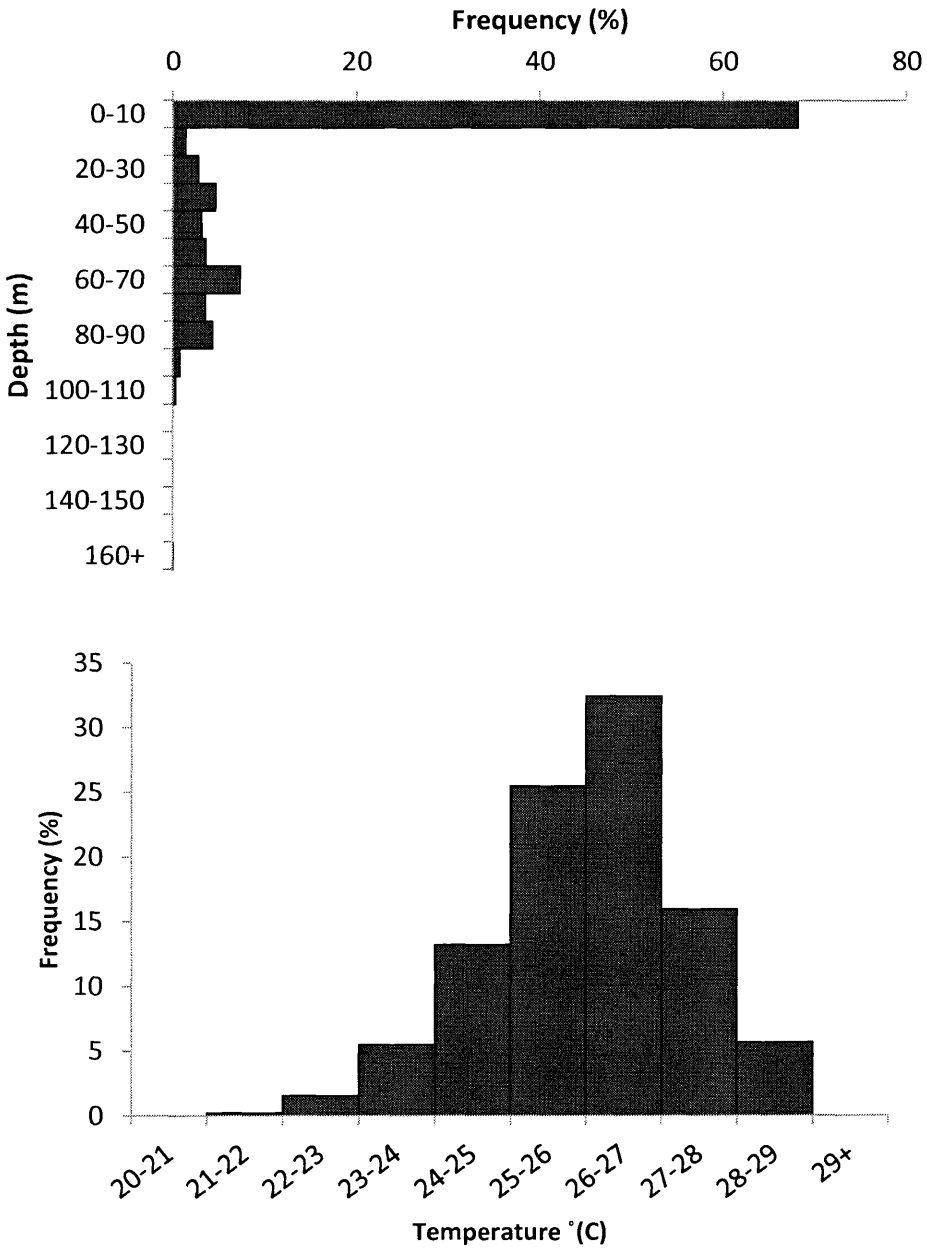


Figure 15: Percent of total time at depth and time at temperature for the roundscale spearfish.

Figure 16: Histograms of percent of total time at depth (m) and at time at temperature (˚C) for WHM 1 over its entire track, and at three different time periods in different geographical locations. (A) August 13, 2011-July 1, 2012, throughout the entire track of the fish. (B) August 13-May 11, the fish remained along the U.S. East Coast throughout the fall, winter, and early spring, and did not make any apparent directed movements. (C) May 11-June 8, the fish made a directed movement nearly due east. (D) June 8-July 1, the fish spent just over one month in the same general area, north of Bermuda.

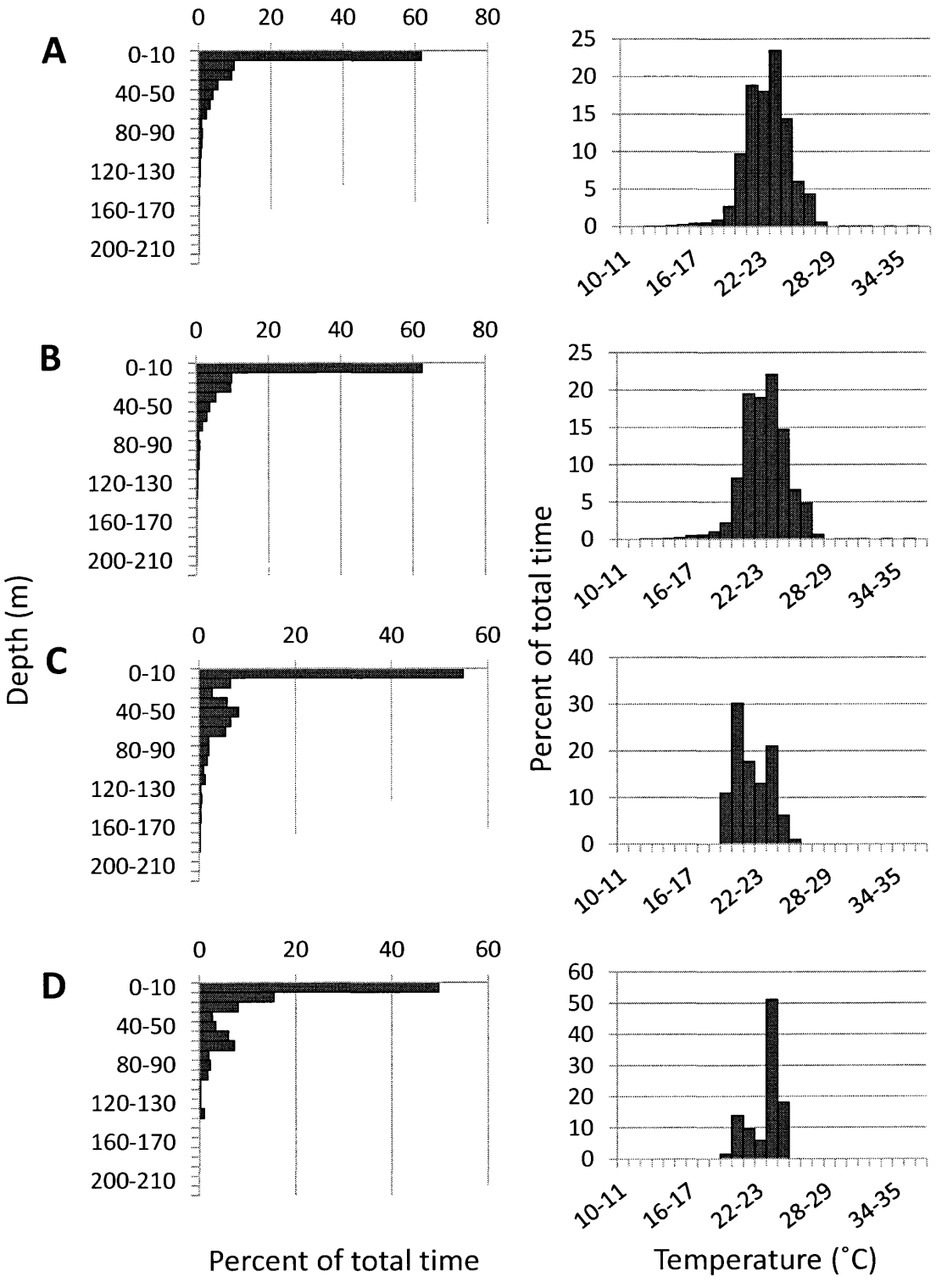
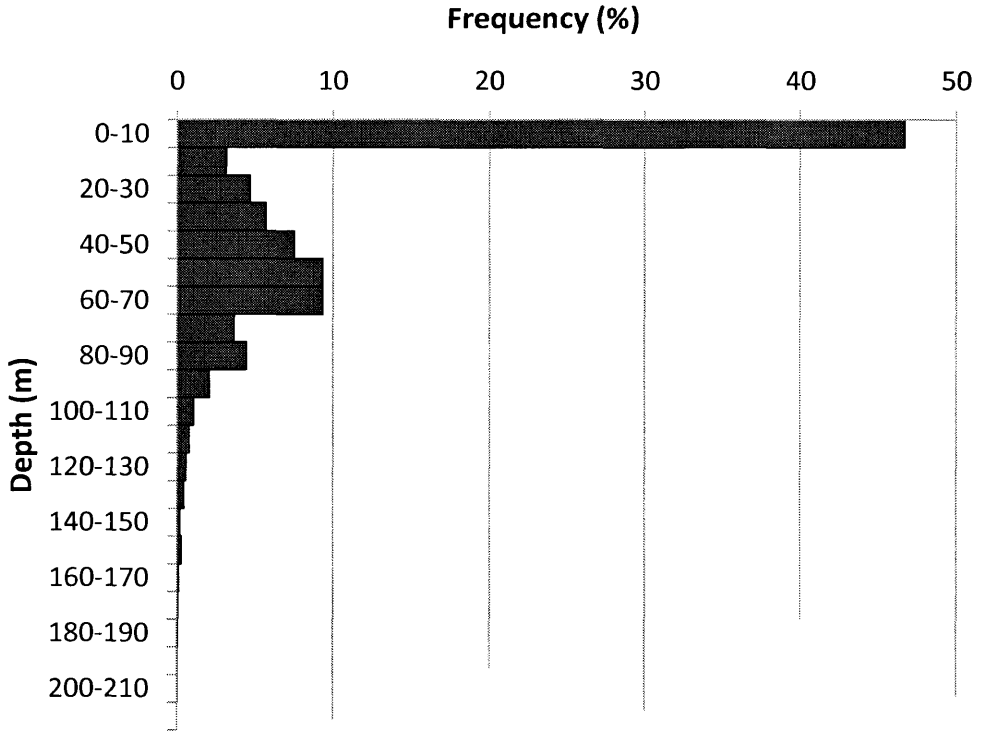

A
B
C
D
0
20
40
60
80
0-10
40-50
80-90
120-130
160-170
200-210
Depth (m)
Percent of total time
25
20
15
10
5
0
40
30
60
50
10-11
16-17
22-23
28-29
34-35
Percent of total time
Temperature (˚C)

Figure 17: Histograms of percent total time at depth (m) and time at temperature (˚C) for WHM 2, throughout the entire year it was tagged, from September 11, 2011-September 11, 2012.


Frequency (%)
0
10
20
30
40
50
Depth (m)
0-10
20-30
40-50
60-70
80-90
100-110
120-130
140-150
160-170
180-190
200-210

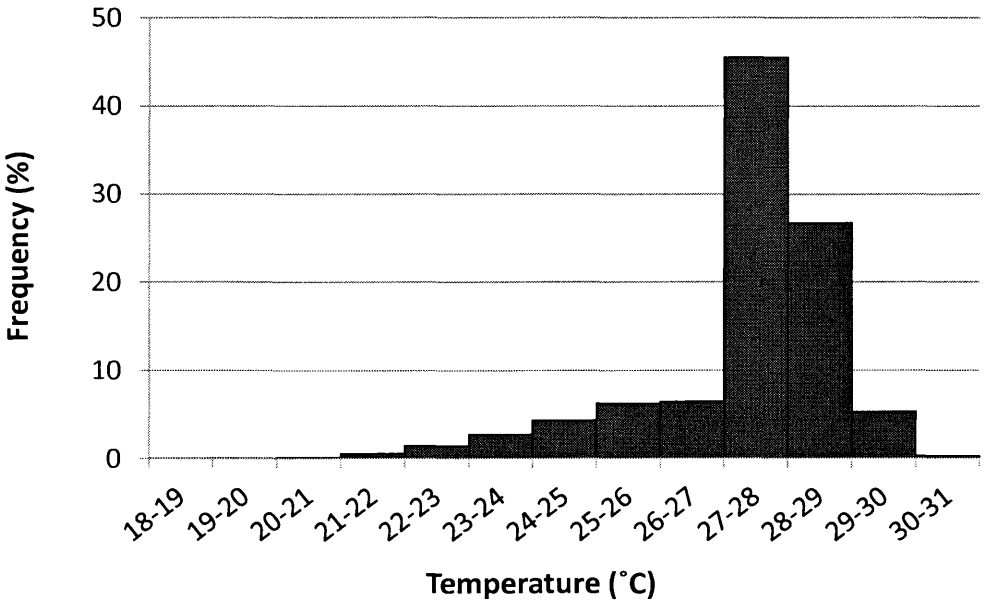
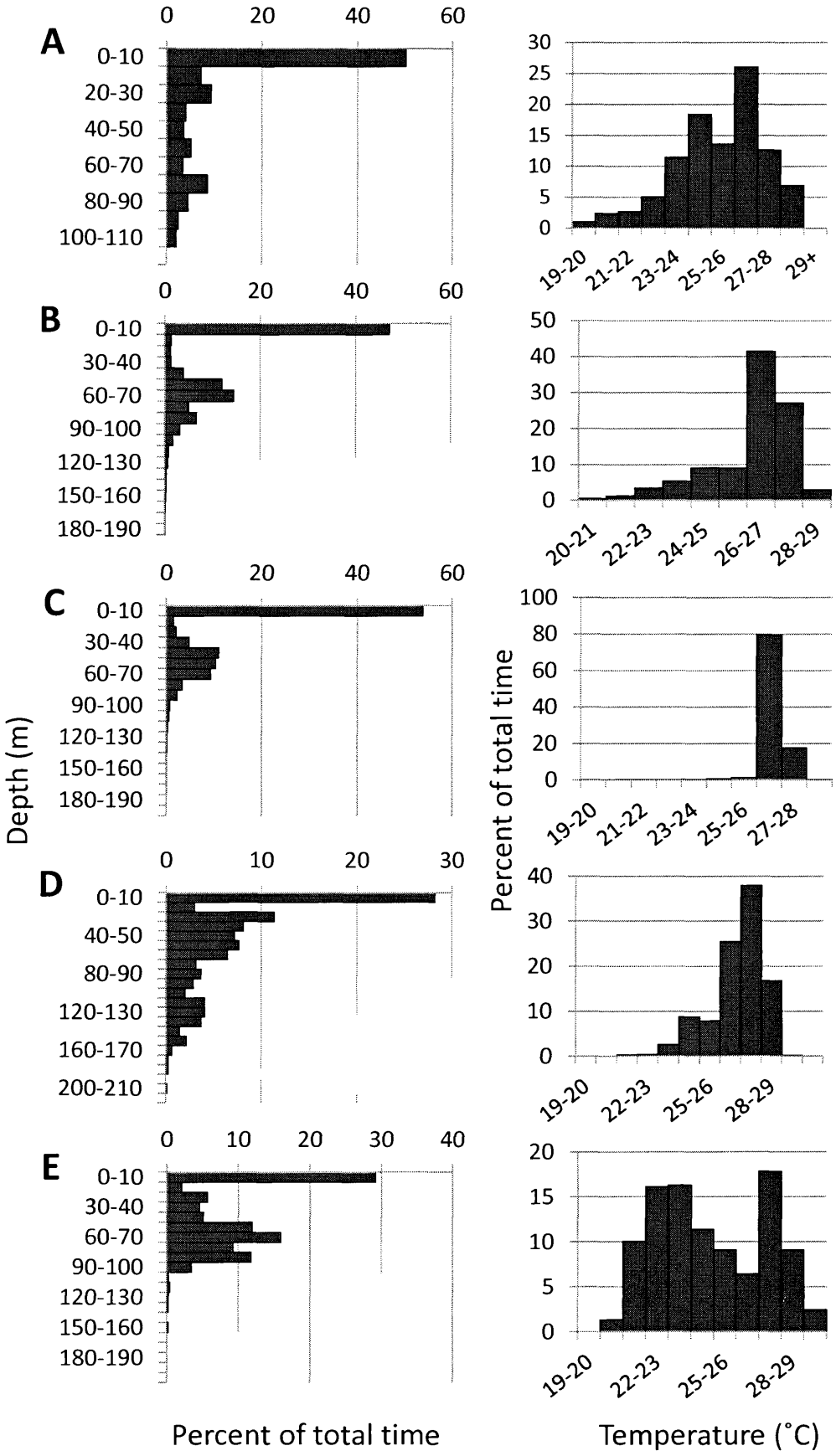

Frequency (%)
50
40
30
20
10
0
18-19
19-20
20-21
21-22
22-23
23-24
24-25
25-26
26-27
27-28
28-29
29-30
30-31
Temperature (˚C)

Figure 18: Histograms of percent of total time at depth (m) and time at temperature (˚C) for WHM 2 at four different time periods in different geographical locations. (A) September 11-September 25, in the Mid-Atlantic Bight. (B) September 26-December 18, when the fish left the Mid-Atlantic Bight and made a directed movement to the southeast. (C) December 19-April 15, when the fish was not making any apparent directed movements, and was off of northern Brazil. (D) May 18-June 22, when the fish was traveling through the Caribbean Sea. (E) June 22-July 15, when the fish was making a directed movement from the Caribbean back toward the Mid-Atlantic Bight.


A
B
C
D
E
Depth (m)
0-10
20-30
40-50
60-70
80-90
100-110
30-40
90-100
120-130
150-160
180-190
160-170
200-210
0
20
40
60
10
30
Percent of total time
19-20
21-22
23-24
25-26
27-28
29+
20-21
22-23
24-25
26-27
28-29
Temperature (˚C)

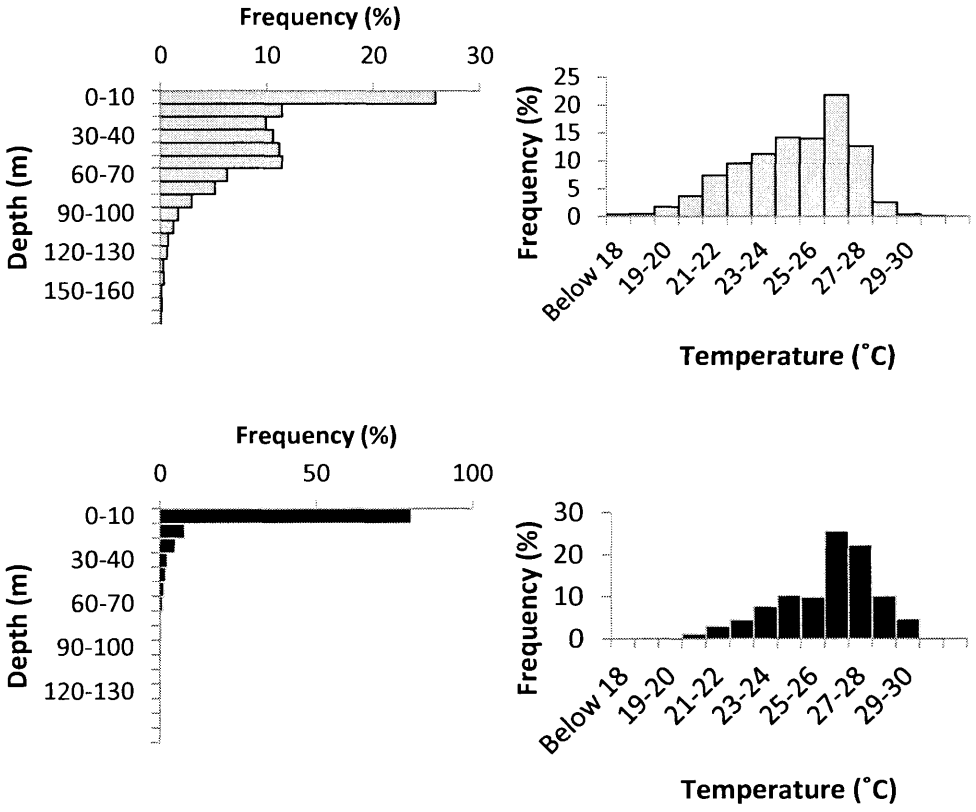


Figure 19: Diel differences in time at depth and time at temperature for all white marlin combined. Percent of total time during daytime hours (top, in grey) and nighttime hours (bottom, in black).

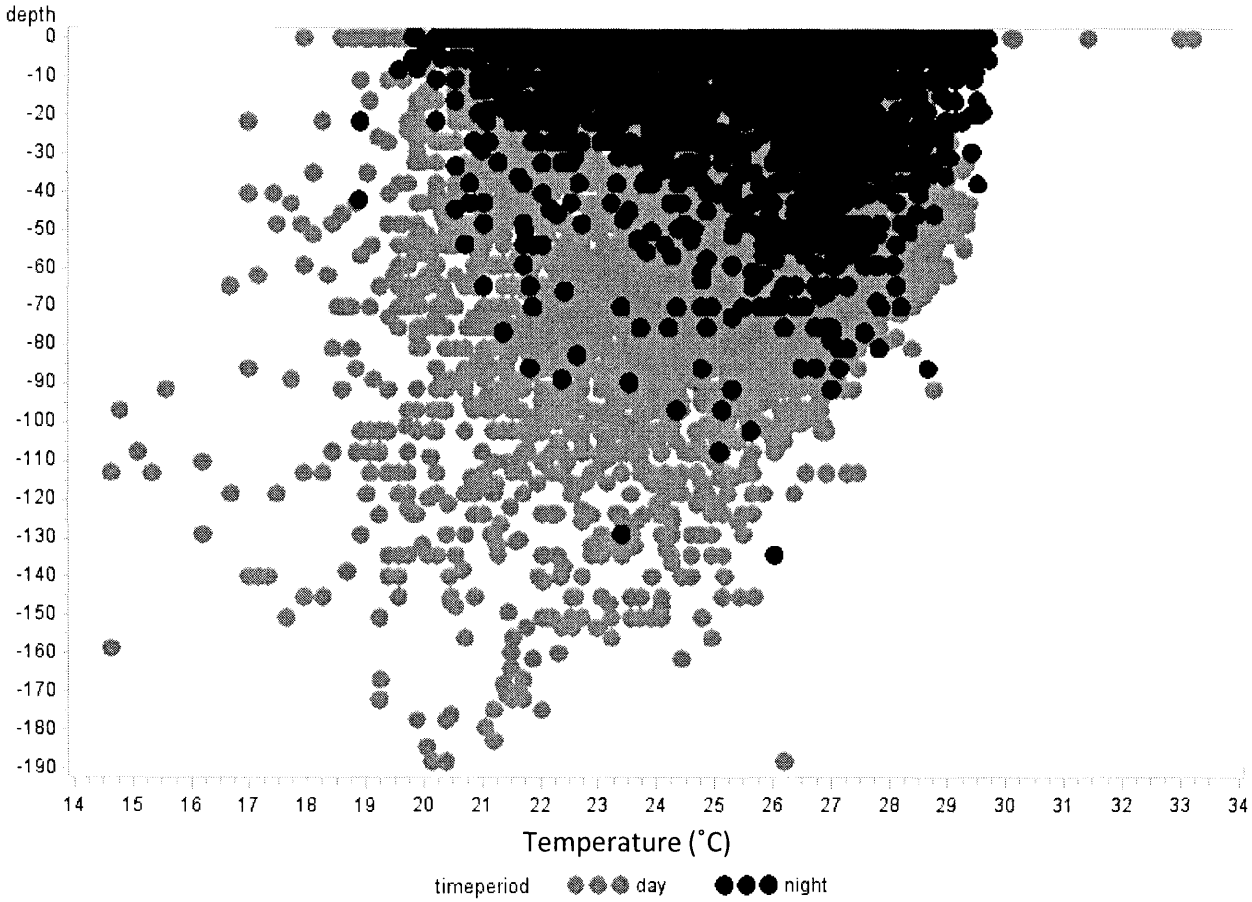


Figure 20: Diel habitat utilization for all white marlin combined. Fish spent significantly more time in deeper waters and cooler temperatures during the day, and shallower waters and warmer temperatures at night.

Chapter 3

Comparative Scale morphology

INTRODUCTION

The use of scale morphology in taxonomic and systematics studies was uncommon until Louis Agassiz published his "Recherches sur les Poissons Fossiles" (Agassiz 1834-1844; Jawad 2005). The first to be credited with taxonomic use of fish scales, Agassiz divided fishes into four categories based on their scale structure: Placoidei, Ganoidi, Ctenoidei, and Cycloidei (Creaser 1926). Although this classification has not withstood scrutiny, Agassiz's work spawned numerous scale studies. This, in conjunction with advances in microscopy in the 1800s and 1900s, allowed for increasingly detailed analyses of scale structure. Cockerell (1912) referred to the study of fish scales as "lepidology", and concluded that the study of scales had great value for the identification and classification of fishes. Although Cockerell had some detractors at the time, it is now commonly accepted that scale morphology can provide valuable phylogenetic and systematic information. The general availability of scales in live, fresh, preserved, and even fossilized fishes only adds to their utility (Roberts 1993).

Several species of Istiophoridae (billfishes) are similar in general appearance, and patterns of squamation have been used to discriminate among billfish species in taxonomic keys of the family (Robins 1974; Nakamura 1985). Of particular relevance to this study is the variation in scale morphology between white marlin (*Kajikia albida*) and roundscale spearfish (*Tetrapturus georgii*), due to their overall

morphological similarity. Scale morphology is only one of several characters used to differentiate between roundscale spearfish and white marlin, with others including relative vent/anal fin placement, presence/absence of spots on the dorsal fin, relative branchiostegal length (Beerkircher 2008), and more recently, head measurements (Beerkircher and Serafy 2011).

In his original description, Lowe (1840) characterized the roundscale spearfish, as being "clothed in large scales of a peculiar shape and nature". Over 130 years later, with little being published on the subject in the intervening years, Robins (1974) concurred with Lowe's description, writing, "Compared to the naked *Xiphias* or to more typical fishes, the long needle-like scales of most istiophorids are indeed peculiar". The peculiarity becomes quite apparent upon examination of roundscale spearfish scales, as their shape varies greatly within and between regions of the fish. Scale morphology of roundscale spearfish is distinct from other istiophorids and especially distinct from most teleosts.

Roundscale spearfish scales are described as being soft and rounded anteriorly, with a few large posterior points, whereas white marlin scales are described as being pointed anteriorly as well as posteriorly (Robins 1974; Nakamura 1985; Shivji et al. 2006). Scales from the lateral surface of the body of the roundscale spearfish have been characterized as being rounded anteriorly, having a broad base, and most commonly having two or three posterior points, although some have only a single point (Beerkircher et al. 2008). These descriptions have been made based on scales from "mid-side" (Robins 1974), "lateral" (Beerkircher

et al. 2008), and "mid-body" (Shivji et al. 2006) scales, which appear to have been sampled arbitrarily, and little mention was made of variation.

Although brief descriptions of scales exist for most istiophorids, a formal study of the variation in squamation patterns within an individual, among individuals of a species, or among the different istiophorids is lacking.

The objective of this study was to investigate squamation patterns of white marlin, including individual scale morphology as well as regional patterns, and variation. Further comparisons between scales of white marlin and those of roundscale spearfish were made to clarify scale morphology spearfish as a possible character for distinguishing the two species.

MATERIALS AND METHODS

Scales were collected from specimens brought to the weigh stations at two billfish tournaments, the White Marlin Open in Ocean City, MD, and both the Ocean City, MD, and Cape May, NJ weigh stations of the Mid-Atlantic $500,000 Tournament in August 2012 and 2013. Because only the largest fish are brought to the weigh station, all scales were sampled from adult fish. A minimum of 10 scales were sampled from each of 11 regions defined by specific anatomical points of reference on each specimen, (1-11; Figure 1). These locations were based on sampling sites from a study of comparative scale morphology and squamation patterns in triplefins (Jawad 2005), as well as personal observation of squamation patterns in billfish specimens in the VIMS Nunnally Ichthyology Collection. In choosing these sampling locations, specific anatomical points of reference were used to ensure that the locations were replicated from one specimen to another to allow accurate and meaningful comparisons.

To remove the scales, a scalpel was used to excise the skin covering the scales, and forceps were used to remove a minimum of 10 contiguous scales from each of the 11 regions of each specimen. Scales were placed in vials of 95% ethanol. Scales were cleaned of soft tissue before being viewed, measured, and photographed with a Zeiss Discovery V20 dissecting photomicroscope. Length and width of the scales were measured and recorded, and length-to-width aspect ratios

were calculated. Scales from three specimens of each species were used for the analyses, due to limitations of roundscale spearfish specimens. Ten scales from each region of each specimen were examined individually and categorized into general groups by shape and distinguishing characteristics. T-tests were performed to quantify potential differences between means of measurements for size comparisons of scales, including length, width, and aspect ratio. These comparisons investigated differences among scales within regions of a species, between regions of a species, and between species. Additionally, an analysis of covariance (ANCOVA) was performed to determine if there is a significant difference in scale length between white marlin and roundscale spearfish. Lower jaw fork length (LJFL) was used as the covariate to determine if there is a significant relationship between scale length and LJFL of the fish.

From three additional sampling locations (A-C), sections of skin tissue (approximately 5x5 cm^2) were removed from each white marlin and roundscale spearfish that were sampled for individual scales. Skin patches were taken from blue marlin for additional comparisons. These patches of skin were kept on ice during sampling, and were later fixed in 10% buffered formalin before being transferred to ethanol for storage. Patches were examined from three specimens each of roundscale spearfish and white marlin, and from one specimen of blue marlin. The patches were cleared in trypsin and stained with alizarin, before being viewed and photographed with the Zeiss Discovery V20 dissecting photomicroscope. The patches were examined to determine the level of imbrication of the scales

within the skin of the fish as well as the overall squamation pattern. The separation space between the scales was compared between species.

Histological sections were prepared from the skin patches from regions A, B, and C from white marlin, roundscale spearfish, and blue marlin. Portions of the skin patches were embedded in paraffin, and were then cut in 8 μm transverse sections with an HM360 microtome. The sections were stained following the Heidenhain-Azan protocol (Romeis 1989), and were later viewed and photographed with an Olympus DP70 camera fitted to an Olympus AX70 microscope.

RESULTS

Skin patches

Two types of ossifications were present in the skin of the three species examined. Near the surface of the skin were small denticular plates, made up of a projecting spine on an irregularly-shaped basal plate. Highly modified cycloid scales were found within the dermis deeply nested below the denticular plates. Denticular plates were present in all of the skin patches sampled, and were located on a very thin layer of the dermis at the surface of the skin that could be peeled back for a clear view of the underlying scales. The density of denticular plates varied greatly between species, as well as between sampling regions within species (Figures 2 and 3). Of the three species, roundscale spearfish (Figure 2 A1, B1, C1; Figure 3A, B) appeared to have the highest density of denticular plates, which were distributed evenly across each individual patch. Blue marlin (Figure 2 A3, B3, C3; Figure 3E, F) had denticular plates in slightly lower densities than roundscale spearfish, and white marlin had the lowest densities, particularly in regions B and C.

In white marlin (Figure 2 A2, B2, C2; Figure 3C, D), higher densities of denticular plates generally occurred in the patches taken nearest the head of the fish, at the anterior base of the dorsal fin (patch A), with the lowest density in the mid-body patch (B). The basal portion of the denticular plates in white marlin, although very irregularly shaped (Figure 3A, B), had a mean width of 0.25 mm

(*SD*=0.04 mm), and a mean length of 0.47 mm (*SD*=0.13 mm). In white marlin, nearly all denticular plates appeared as individual plates in contrast to the other species, in which each denticular plate supported numerous denticles suggesting fusion between plates (Figure 3D, F).

Roundscale spearfish had nearly equal densities of denticular plates across all three of the sampled areas, although the denticular plates varied in their overall shape (Figure 3C). Some of the plates appeared as though they were in irregular lines (i.e., chains), joined by the basal plates, while others appeared individually. The basal plates (Figure 3D) in roundscale spearfish had a mean width of 0.14 mm (*SD*=0.04 mm). Length of the plates in roundscale spearfish was not measured due to the appearance of the chains, making it difficult to determine where one ended and the next one began. The spines on the denticular plates averaged 0.03 mm (*SD*=0.005) in diameter. In addition to the chains of denticular plates, the spines and the plates appeared thicker in roundscale spearfish, and the spines appeared more substantial, than those in white marlin and blue marlin.

Denticular plates in blue marlin appeared in slightly lower densities than in roundscale spearfish, and had a mean width of 0.19 mm (*SD*=0.04 mm) and a mean length of 0.36 mm (*SD*=0.06 mm). The spines on the denticular plates averaged 0.04 mm (*SD*=0.01 mm) in diameter. The denticular plates appeared in roughly equal densities in all patches. The plates were primarily independent, although it was not uncommon to find two to four plates joined together. However, the long chains of plates that were present in roundscale spearfish were not observed in blue marlin.

In all three species, the scales were located deeper than and completely separate from the denticular plates (Figure 4), with varying degrees of imbrication. The structure of the scales varied greatly between species, between the sampled regions, and even within sampled regions. In all species examined, scales were located well below the surface of the skin, with the anterior ends in scale pockets that were completely transparent in the cleared and stained skin patches. While still covered by the dermis, the posterior ends of the scales projected nearer to the surface of the skin than the anterior ends due to the imbrication of the scales. This was more evident in white marlin due to the heavily imbricated nature of their scales compared to either roundscale spearfish or blue marlin. However, all three species tended to have more heavily imbricated scales in region A than in regions B or C. In regions B and C scales were particularly openly spaced in roundscale spearfish. In roundscale spearfish there was generally space around the scales, with only the posterior points from the previous scale overlapping the anterior end of the next scale, if they overlapped at all. Blue marlin scales were less imbricated than white marlin, but more so than roundscale spearfish. With some space around blue marlin scales, only slightly more overlap was present than in roundscale spearfish scales (Figure 2).

Squamation patterns

The cleared and stained skin patches revealed squamation patterns of white marlin, roundscale spearfish, and blue marlin in sampling regions A, B, and C (Figure

2). In white marlin, scales located on the dorsal surface below the highest point of the dorsal fin (region A), were the most heavily imbricated and elongate, with single anterior and posterior points. Scales in on the dorsal surface of the mid-body (region B) and along the lateral line just anterior to the insertion of the second anal fin (region C) were both generally less imbricated than those in region A. Scales in regions B and C were primarily elongate with a few deeply forked scales randomly interspersed among the others. Patterns in regions B and C varied between specimens in the actual arrangement of the scales, with some appearing to be in orderly lines, while others appeared more haphazardly arranged.

In roundscale spearfish, scales in region A were the most heavily imbricated, with and were of various forms. Most scales were pointed anteriorly and posteriorly, and were wider than the same region in white marlin. Scales in regions B and C in roundscale spearfish were considerably less imbricated, with obvious space around each scale. In these areas of the body, the points of the scales only overlapped slightly, if at all. Scales in regions B and C were generally rounded anteriorly. The posterior points were irregular and varied, with most scales having one to three posterior points and with a few scales having five or six.

The pattern of more heavily imbricated scales in region A was noted for blue marlin as well. These scales were narrow and elongate. Regions B and C in blue marlin were again more similar to each other than to region A, and were characterized by scales that were rounded anteriorly and generally had a single posterior point.

Individual scales

Scale length and width frequency histograms for white marlin and roundscale spearfish are presented in Figure 5.

White marlin mean scale length (range 12.2-22.2 mm, overall mean of 16.5 mm) was greater than that of roundscale spearfish in all regions except region 1 (Figure 6). Roundscale spearfish mean scale length ranged from 9.80-22.0 mm, with an overall mean of 14.4 mm. White marlin mean scale width was less than that of roundscale spearfish for all regions except region 1, in which it was just slightly greater than that of roundscale spearfish (Figure 7). Mean scale width of white marlin by region ranged from 1.20-3.39 mm, with an overall mean of 1.73 mm, while roundscale spearfish scale width by region ranged from 1.59-3.74 mm, with a mean of 2.59 mm across all regions. Mean aspect ratio of scale length-to-width was greater for white marlin in all regions except region 1 (Table 1 and Figure 8). In general, white marlin had more elongate and narrow scales than roundscale spearfish. In region 1, however, roundscale spearfish had extremely elongate and narrow scales, which were not seen in any other region of this species. Aspect ratios of white marlin scales across all regions ranged from 5.8-17.4, with an overall mean of 10.5, while aspect ratios of roundscale spearfish scales by region ranged from 3.6-14.2, with an overall mean of 6.6.

Means of scale length, width, and aspect ratio suggested general trends across the regions in both species (Figures 6, 7, 8). In all three of these graphs, as

the means increase or decrease in one species, the other generally increases or decreases as well.

Means and standard deviations of scale length, width, and length-to-width aspect ratios, as well as a description of level of morphological variation among scales by region are presented in Table 1 for white marlin and Table 2 for roundscale spearfish. The level of morphological variation was determined by a qualitative assessment of the number of different scale shapes present in each region, with one or two shapes being considered low, three or four shapes being considered moderate, and five or more shapes being considered high.

White marlin scale length ($\overline{L}$= 16.5 mm; *SD*=2.8) across all regions was not significantly different (p=0.08) from roundscale spearfish scale length ($\overline{L}$=14.4 mm; *SD*=2.8). Scale width was significantly different (p=0.005), with roundscale spearfish ($\overline{W}$=2.59 mm; *SD*=0.67) exhibiting greater scale width than white marlin ($\overline{W}$=1.73 mm; *SD*=0.37 mm). T-tests of mean aspect ratios (scale length/scale width) for each region of each species showed a significant difference between white marlin and roundscale spearfish (p <0.001), with the aspect ratio of white marlin being greater ($\overline{AR}$=10.5; *SD*=2.4) than that of roundscale spearfish ($\overline{AR}$=6.6; *SD*=2.2).

Morphological descriptions of scales by region

Although the scales within every region sampled exhibited considerable qualitative morphological variation, regions were typically characterized by the

presence of a few primary scale shapes. In the following descriptions of scale morphology by region, I focus on these major scale shapes.

White marlin individual scales by region (Figure 9)

Region 1: Nearly all scales from region 1 were elongate with points at both ends, although a few were moderately forked posteriorly. Approximately half of the scales were slightly curved, while the other half were straight. The scale lengths in region 1 ranged from 9.5-31.1 mm ($\overline{L}$=18.7 mm; *SD*=6.0 mm), widths from 1.-2.3 mm ($\overline{W}$=1.6 mm, *SD*=0.3 mm), and the mean length-to-width aspect ratio was 11.9.

Region 2: Scales in this region were difficult to categorize due to the extent of morphological variation. Approximately 25% of the scales had anterior ends that were largely rounded, but with a very fine, sharp point (Figure 9, 2D); these scales generally had a single posterior point. Another 25% of the scales had multiple short points anteriorly, while posteriorly, these scales were either widely and unevenly forked, or had up to four longer posterior points. Scales with multiple posterior points in this region were very irregularly shaped. Of the scales with anterior points, approximately 25% were widely forked posteriorly, with two to three points per fork. Roughly half of the scales sampled had pointed ends both anteriorly and posteriorly, but anteriorly the scales widened slightly before tapering to a single posterior point. The scale lengths in region 2 ranged from 13.4-27.7 mm

($\overline{L}$=18.7 mm; *SD*=3.6 mm), widths from 2.0-6.5 mm ($\overline{W}$=3.4 mm, *SD*=1.1 mm), and the mean length-to-width aspect ratio was 5.8.

Region 3: Most scales in this region were elongate and pointed on both ends. Approximately 25% had semi-rounded ends with a very short and narrow point anteriorly, while another 25% were semi-rounded anteriorly without the point. Roughly 10% of the scales had two to four posterior points and were widest in the body of the scale just before the points branched off individually. A few scales in this region were thick and deeply forked. The scale lengths in region 3 ranged from 13.9-24.5 mm ($\overline{L}$=18.8 mm; *SD*=2.2 mm), widths from 1.5-3.2 mm ($\overline{W}$=2.1 mm, *SD*=0.4 mm), and the mean length-to-width aspect ratio was 9.4.

Region 4: Nearly all sampled scales in region 4 were elongate and pointed at both ends. Approximately half of the scales were fairly even in width throughout the middle section, tapering evenly at both ends. The other half had a wider anterior end, then tapered in and back out near the middle of the scale, before narrowing again to a single posterior point. The scale lengths in region 4 ranged from 15.7-22.9 mm ($\overline{L}$=19.1 mm; *SD*=1.7 mm), widths from 1.1-1.8 mm ($\overline{W}$=1.4 mm, *SD*=0.15 mm), and the mean length-to-width aspect ratio was 14.0.

Region 5: Most scales in this region were moderately elongate, with both ends pointed. Approximately half were slightly curved, while the others had a straighter form. Nearly 25% had a slightly rounded anterior end, before tapering back to a single point. A few were moderately to widely forked; one was widely

forked in a deep "V". The scale lengths in region 5 ranged from 9.2-19.1 mm ($\overline{L}$=13.5 mm; *SD*=1.9 mm), widths from 1.6-4.6 mm ($\overline{W}$=2.5 mm, *SD*=0.5 mm), and the mean length-to-width aspect ratio was 9.4.

Region 6: Most scales in this region were wider toward the anterior end, and then tapered back to a single posterior point. Approximately one half were slightly rounded at the anterior end, and very few were forked. This region seemed to represent the same squamation pattern as seen in some of the skin patches, where most of the scales were elongate and pointed anteriorly and posteriorly, although forked scales were occasionally present. The scale lengths in region 6 ranged from 9.4-16.7 mm ($\overline{L}$=12.3 mm; *SD*=1.2 mm), widths from 2.2-5.3 mm ($\overline{W}$=3.4 mm, *SD*=0.6 mm), and the mean length-to-width aspect ratio was 8.9.

Region 7: Nearly 75% of the scales in this region were elongate and narrow, with both ends pointed. An additional 25% were extremely elongate and narrow, and had a lanceolate shape. Nearly all scales in this region had a single posterior point, except for a few that were forked. The scale lengths in region 7 ranged from 13.1-27.9 mm ($\overline{L}$=18.4 mm; *SD*=3.2 mm), widths from 1.1-2.7 mm ($\overline{W}$=1.8 mm, *SD*=0.4 mm), and the mean length-to-width aspect ratio was 17.4.

Region 8: Nearly all scales in region 8 were pointed at both the anterior and posterior ends with a slightly thicker middle section, and tapered toward both ends. Approximately 30% of the scales were slightly curved while nearly 60% were straight. A few moderately forked scales were also present. The scale lengths in

region 8 ranged from 5.8-22.0 mm ($\overline{L}$=11.2 mm; *SD*=3.2 mm), widths from 0.8-3.2 mm ($\overline{W}$=2.1 mm, *SD*=0.6 mm), and the mean length-to-width aspect ratio was 10.9.

Region 9: Scales in region 9 exhibited a number of morphological variations. Nearly 75% of the scales were relatively short with pointed anterior and posterior ends, although approximately one quarter were slightly rounded anteriorly with a single posterior point. A few were widely forked at the halfway point, and even fewer had two posterior points that only split in two very close to the end. Approximately one half of the widely forked scales were unevenly forked, with one side of the fork being distinctly shorter than the other. The scale lengths in region 9 ranged from 7.5-15.3 mm ($\overline{L}$=10.2 mm; *SD*=0.63 mm), widths from 1.7-5.6 mm ($\overline{W}$=2.9 mm, *SD*=1.4 mm), and the mean length-to-width aspect ratio was 7.8.

Region 10: Scales in region 10 were elongate, and nearly all were pointed at both ends. A few had slightly rounded anterior ends, but were narrow and tapered to a sharp point at the posterior end; a few moderately forked scales were present. The scale lengths in region 10 had lengths that ranged from 5.7-21.1 mm ($\overline{L}$=13.7 mm; *SD*=3.2 mm), widths from 0.5-3.0 mm ($\overline{W}$=1.8 mm, *SD*=0.48 mm), and the mean length-to-width aspect ratio was 12.6.

Region 11: Scales in region 11 varied from elongate and pointed at both ends with the thickest portion occurring in either the anterior half of the scale or in the middle section (approximately 25% of the scales), to shorter scales that were irregularly shaped, but generally pointed at both the anterior and posterior ends

(approximately 75% of the scales). A few scales appeared almost diamond-shaped, and a few moderately forked scales were present. The main body of these forked scales was short, with elongate points to the forks. The scale lengths in region 11 ranged from 5.4-14.9 mm ($\overline{L}$=9.8 mm; *SD*=2.3 mm), widths from 1.4-5.7 mm ($\overline{W}$=2.7 mm, *SD*=0.77 mm), and the mean length-to-width aspect ratio was 7.9.

Roundscale spearfish individual scales by region (Figure 10)

Region 1: Approximately 75% of the scales in region 1 were elongate and widest in the middle, then tapered anteriorly and posteriorly toward both ends, while having a slight curve. The remaining scales were rounded anteriorly with a single posterior point. The scale lengths in region 1 ranged from 7.0-33.5 mm ($\overline{L}$=21.9 mm; *SD*=7.1 mm), widths from 0.9-2.4 mm ($\overline{W}$=1.6 mm, *SD*=0.27 mm), and the mean length-to-width aspect ratio was 14.2.

Region 2: Scales in region 2 exhibited high morphological variation. Nearly half of the scales were rounded anteriorly, and of those approximately half had a single posterior point, while the other half forked dramatically. Approximately 10% of the scales had jagged and irregular anterior edges or points (or both), and up to five jagged posterior points. Another 10% were rounded anteriorly, but split into a deep and wide "V". Another 10% were short and wide, with two to five posterior points that had a feathery appearance. The remaining scales exhibited a mixture of the characters described in the other scales, and did not have a specific overall

shape. The scale lengths in region 2 ranged from 7.2-25.0 mm ($\overline{L}$=17.2 mm; *SD*=3.6 mm), widths from 1.6-8.8 mm ($\overline{W}$=3.7 mm, *SD*=1.3 mm), and the mean length-to-width aspect ratio was 5.0.

Region 3: Approximately half of the scales in region 3 had varying degrees of rounded anterior ends. Some were rounded, while others appeared blunt or had a slight point, with 3-5 posterior points. Approximately half of the scales in this region were wider, and exhibited a human footprint-like shape, with typically 4-6 posterior points forming toe-like projections. The maximum width for most scales occurred at the base of the points, rather than at the main body of the scale. The scale lengths in region 3 ranged from 11.8-20.7 mm ($\overline{L}$=13.7 mm; *SD*=2.0 mm), widths from 1.8-10.0 mm ($\overline{W}$=3.5 mm, *SD*=1.2 mm), and the mean length-to-width aspect ratio was 5.1.

Region 4: Nearly all scales sampled from region 4 were rounded anteriorly to some degree, although a few came to thick points, while the posterior points varied. Approximately half of the scales were rounded anteriorly with multiple posterior points (mostly 2-3), while most of the other half had a rounded anterior end with a single posterior point. The scales with a single posterior point were widest at approximately one-quarter of the way from the anterior margin of the scale, before gradually tapering back to a point. A few scales had a single, slightly rounded anterior end which broadened out to the widest point near the midpoint of the scale. They then tapered back to a sharper posterior point. The scale lengths in

region 4 ranged from 8.5-17.6 mm ($\overline{L}$=14.1 mm; *SD*=1.5 mm), widths from 1.5-4.0 mm ($\overline{W}$=2.6 mm, *SD*=0.61 mm), and the mean length-to-width aspect ratio was 5.9.

Region 5: Nearly all scales in region 5 had rounded to semi-rounded anterior ends. A few of the scales had a small point projecting from an otherwise rounded anterior end. Approximately half were club-like in shape, with a rounded anterior end and a single, long posterior point (approximately two-thirds the length of the scale), although a few had two posterior points. The scale lengths in region 5 ranged from 9.2-19.4 mm ($\overline{L}$=13.5 mm; *SD*=1.9 mm), widths from 1.6-4.6 mm ($\overline{W}$=2.5 mm, *SD*=0.50 mm), and the mean length-to-width aspect ratio was 5.7.

Region 6: Similar to region 3, a few of the scales in region 6 had a human footprint shape, while approximately 10% appeared more like a human handprint. A few of these had a single point protruding laterally at an angle of approximately 60° to the main body of the scale. More than half of the scales were generally rounded anteriorly, some with a very small point on the anterior tip. Most of these had two or three long posterior points. Approximately 10% of the scales were triangular, with one or two long posterior points that were roughly half the length of the scale. A very few were the "typical" roundscale spearfish scale described from previous studies with a rounded anterior end, tapering back to a single posterior point. The scale lengths in region 6 ranged from 9.4-16.7 mm ($\overline{L}$=12.3 mm; *SD*=1.3 mm), widths 2.2-5.3 mm ($\overline{W}$=3.4 mm, *SD*=0.62 mm), and the mean length-to-width aspect ratio was 3.8.

Region 7: Nearly all scales in region 7 were elongate with a single posterior point. These varied from being sharply pointed to rounded anteriorly; but all were pointed posteriorly. Nearly all of these scales were widest for the first half of the scale, and then tapered back to a posterior point. A few scales sampled from this region were forked posteriorly. This appeared to be a typical squamation pattern, as some of the cleared and stained patches primarily contained scales with single anterior and posterior points, with a forked scale randomly interspersed. The scale lengths in region 7 ranged from 13.1-27.9 mm ($\overline{L}$=18.4 mm; *SD*=3.2 mm), widths from 1.1-2.7 mm ($\overline{W}$=1.8 mm, *SD*=0.97 mm), and the mean length-to-width aspect ratio was 10.8.

Region 8: Nearly all of the sampled scales for region 8 were rounded anteriorly, tapering back to a single posterior point. The rounded portion extended approximately one-third to one-half the length of the scale before tapering posteriorly. The remaining scales were primarily elongate with two long posterior points. There were a few that were much shorter and almost diamond-shaped. The scale lengths in region 8 ranged from 5.8-22.0 mm ($\overline{L}$= 11.2mm; *SD*=3.2 mm), widths from 0.8-3.82 mm ($\overline{W}$=2.1 mm, *SD*=0.57 mm), and the mean length-to-width aspect ratio was 6.0.

Region 9: Scales from region 9 were generally rounded anteriorly, with one to four posterior points. These scales were typically wide; approximately 25% were human hand-shaped, with the "fingers" being the posterior points, while others

varied in the length and shape of the posterior points. In roughly 30% of the scales, the main body of the scale was two-thirds the overall length, while another 30% had posterior points that made up nearly two-thirds of the overall length. The remaining scales were diamond shaped. The scale lengths in region 9 ranged from 7.5-15.3 mm ($\overline{L}$=10.2 mm; *SD*=1.4 mm), widths from 1.7-5.6 mm ($\overline{W}$=2.9 mm, *SD*=0.63 mm), and the mean length-to-width aspect ratio was 3.6.

Region 10: Although some had pointed ends, approximately 60% of the scales in region 10 were elongate, and generally had a rounded anterior end. Scales in this region with a rounded anterior end tended to be longer than similarly shaped scales in other regions. Most of the remaining 40% of the scales were rounded anteriorly but split into two or three posterior points, with some having a form that is elongate and just slightly rounded. A few were completely forked in a deep "V". The scale lengths in region 10 ranged from 5.7-21.1 mm ($\overline{L}$=13.7 mm; *SD*=3.2 mm), widths that ranged from 0.5-3.0 mm ($\overline{W}$=1.8 mm, *SD*=0.48 mm), and the mean length-to-width aspect ratio was 8.6.

Region 11: This region contained a great deal of variation. One specimen had scales in this region that were tiny and irregular, appearing broken (Figure 10, 11A). Due to their appearance, and the morphological differences between this specimen and the others, it is possible that this specimen had regenerated the scales near its caudal peduncle. Of the other specimens, roughly 60% of the scales in this region were rounded, semi-squared, or diamond-shaped for the anterior one-third

to one-half of their length. They generally tapered back to a single point, although a few had two or three points. These scales varied in length with some being very short and wide anteriorly, while others were twice their length. The remaining 40% of the scales were more elongate, but still exhibited a wider anterior end with a trailing point. The scale lengths in region 11 ranged from 5.4-14.9 mm ($\overline{L}$=9.8 mm; *SD*=2.3 mm), widths from 1.4-5.7 mm ($\overline{W}$=2.7 mm, *SD*=0.77 mm), and the mean length-to-width aspect ratio was 3.9.

Results from the analyses of covariance (ANCOVA) investigating the relationships of scale length with species (WHM vs. SPG) suggested that species was associated significantly with scale length $F(1,1305) = 27.9$, $p = <0.0001$. The covariate, LJFL, was not significantly related to the scale length $F(2,1305) = 2.6$, $p = 0.11$.

DISCUSSION

There have been relatively few studies of istiophorid scales or intraspecific variation of scale morphology. Nonetheless, scale morphology has been considered to be a reliable character for differentiating between species (e.g. Nakamura 1985). Several studies have reported on the morphological differences between roundscale spearfish and white marlin, and the shape of scales from areas on the sides of these fishes has been used for distinguishing between the species. Descriptions in the literature focus on scales sampled from "below the spinous dorsal fin" (Robins 1974: p 59), on the "sides of body" (Nakamura 1985: p 45), on the "mid-lateral side of each animal a few centimeters behind the pectoral fin" (Shivji et al. 2006: p 485), and "about five cm above and below the lateral line, at a position about midway under the pectoral fin", where they were sampled "haphazardly" (Beerkircher et al. 2008: p 156). All of these studies describe roundscale spearfish scales as being rounded anteriorly and soft, and reveal only a few more general observations: "with few large posterior points" (Robins 1974: p 57), "only slightly imbricated" (Nakamura 1985: p 45), "with two to three posterior points" (Shivji et al. 2006: p 485) or "invariably broad based...most commonly there are 2-3 points; however some scales only have single points" (Beerkircher et al. 2008: p 162).

Although these studies were the first to examine scale morphology of roundscale spearfish in comparison to other istiophorids, they represented only a

small number of scales sampled from one imprecise location on the lateral surface of the mid-body of the fish, and described a single general scale shape for each species. In doing so, previous studies overlooked a vast morphological variation of scales present throughout different regions of the fish. I examined eleven distinct regions, spaced from head to tail, in order to represent the scale morphology of the entire fish and to provide a more comprehensive analysis of the scales on the body of the roundscale spearfish and white marlin. Of those who studied roundscale spearfish specimens and their scales, only Robins (1974) examined scales from beyond the mid-body lateral area. He described scales from the dorsal and ventral parts of the body as being elongate, imbricated, and stiff. This matches my observations of these regions.

White marlin have considerably less overall morphological variation of individual scales than roundscale spearfish, although they had considerably more variation than has been described in the literature. Both species had morphological differences within and among regions. Regions 4, 7, and 10 (all ventral regions), were similar in that they contained elongate scales, the majority of which were pointed on both ends; however, region 1, which was ventral and directly below the highest point of the dorsal fin, also had similarly shaped scales. Scales from regions 1, 4, 7, and 10 exhibit the characteristics previously described for white marlin. Robins (1974) described white marlin scales as being pointed and pungent, and Shivji et al. (2006) described them as being pointed at the anterior end with one or two posterior points. Regions 5, 6, 8, and 9 were also similar to each other. Regions

5 and 8 were both dorsal, with region 5 being in a straight line up from the insertion of the first anal fin, and region 8 located in a straight line up from the insertion of the second anal fin. Region 6 was directly below region 5, just below the lateral line, and region 9 was just below 8, below the lateral line. All four of these regions had predominately shorter, slightly wider scales, although each region had additional scale shapes that were not present in all of the other regions. Regions 2 (directly posterior to the center of the opercle) and 3 (ventral to the insertion of the pectoral fin) each had a great deal of morphological variation, but also had some scale shapes in common with other regions.

Roundscale spearfish scales were found to have much greater morphological variation than white marlin scales, and considerably greater variation than previously described in the literature. Past studies describe the lateral mid-body scales as rounded, with few large posterior points (Robins 1974), rounded anteriorly and only slightly imbricated (Nakamura 1985), and notably rounded anteriorly with two to three posterior points (Shivji et al. 2006). Because they focused on this single lateral mid-body region, these studies overlooked many of the scale forms entirely. This included some of the more unusual forms such as elongate scales from the dorsal surface, scales with anterior points, those with five or more posterior points, and scales shaped like human footprints or hands.

In the present study, sampling regions 3 (ventral to the insertion of the pectoral fin) and 4 (ventral and anterior to the pectoral fin) on roundscale spearfish revealed some scales that were morphologically similar; specifically scales that were

rounded anteriorly with multiple posterior points. Additionally, regions 5 and 6 (mid-body ventral and mid-body below the lateral line, respectively) had some similarly shaped scales, including scales that were rounded anteriorly with a single posterior point, which were also present in region 8 (dorsal at insertion of second anal fin). However, each of these three regions contained additional scale shapes that were not present in the other regions. Finally, scales in regions 6, 9, and 11 (all three just below the lateral line, at mid-body, in line with the insertion of the second anal fin, and near the caudal peduncle, respectively), exhibited morphological similarities. These regions contained scales that were diamond-shaped, and were wide anteriorly.

Between species comparison

Roundscale spearfish tended to have a greater variety of scale shapes within each region than white marlin. The majority of general scale shapes seen in white marlin were present in roundscale spearfish; although the reverse was not true. Scales from roundscale spearfish were noticeably shorter and wider in most regions, were much more frequently rounded anteriorly than those of white marlin, and often had a greater number of posterior points. Roundscale spearfish regions 3, 4, 5, 6, 8, 9, and 11 were characterized by a vast assortment of morphological forms that were not seen in white marlin. White marlin ventral regions 3, 4, 7, and 10 (as well as dorsal regions 1 and 8) were generally characterized as having narrow, elongate scales with anterior ends varying from semi-rounded to sharply pointed,

and generally had a single sharp posterior point, which was similar to scales from dorsal region 1 and ventral region 7 in roundscale spearfish. Mean scale length, width, and aspect ratio differed between species for each region, and there were pronounced differences, particularly in aspect ratio, for the majority of regions (Tables 1 and 2).

As previous descriptions suggest, when viewed superficially on the lateral surface of the fish without the aid of a microscope, roundscale spearfish scales appear rounded anteriorly and generally taper to a single posterior point. In contrast, white marlin scales appear narrow and pointed at both ends. Although these descriptions provide a general overview of scales in this lateral mid-body area, they overlook some of the morphological variation revealed by closer examination. For example, as described for white marlin, the scales in this area are generally narrow and elongate with a single anterior and posterior point. There are, however, also forked scales interspersed among the others. In contrast, in roundscale spearfish this area is generally characterized by scales that are rounded anteriorly with a single posterior point, although there are variations in aspect ratio, as well as in the number of posterior points. Additionally, outside of this one general area, which had been examined in previous studies, there is much greater morphological variation than has been described previously. The scales of roundscale spearfish and white marlin show extensive morphological variation within individual specimens of each species, as well as between the two species, as described above. Despite the morphological differences, there are enough similarities between scales of

roundscale spearfish and white marlin that individual scales from these fish cannot be reliably used to distinguish between the two species. However, along with other distinguishing characters, general squamation patterns in specific regions remain useful for field identification of white marlin and roundscale spearfish, which are frequently misidentified. Scales from the lateral section of the body posterior to the operculum have typically been used for this purpose, and this remains a reliable method for distinguishing between the two species. In addition to the general descriptions of scales present in this area, perhaps the most notable distinction between the two species is the stippled appearance of the roundscale spearfish scales, which is a result of the rounded anterior ends, and the lack of imbrication among the scales. Indeed the common name "roundscale spearfish" was suggested by Robins (1974) in recognition of these unique lateral scales (Figure 2, B2). In contrast, white marlin scales from the same lateral region are heavily imbricated and appear as overlapping and needle-shaped (Figure 2, B1).

Scales in the istiophorids I examined were fully embedded in the dermis, as has been documented for other species. For some time, there was confusion in the literature regarding the presence of scales in adult swordfish (*Xiphias gladius*). Govoni et al. (2004) showed that scales are present in adult swordfish; however, the thickening of the dermis throughout ontogeny results in scales of adults becoming more deeply embedded in the dermis, with only the tips of the spines protruding through the dermis. A similar pattern could be occurring in istiophorids, as it is not

known if the embedded scales represent the terminal condition, and if perhaps they are more superficial earlier in ontogeny.

Denticular plates

Ossifications similar to the denticular plates I have described were previously reported as being present in *Makaira ampla* and *Makaira albida* [synonyms of *Makaira nigricans* (blue marlin) and *Kajikia albida* (white marlin), respectively] by La Monte (1958). This author referred to them as "surface scales", which are tiny and scattered over the dermis of the adult. They occur on the outermost surface of the fish, and are completely separated from the actual scales, which La Monte (1958) referred to as the "subcutaneous scales". I observed denticular plates in all three istiophorid species examined. Histological slides (Figure 4) illustrate the separation of the denticular plates and the actual scales.

It is possible that denticular plates have a hydrodynamic function. Ctenoid scales have been described as being very similar to cycloid scales, with the addition of small spines called cteni at their posterior edges. Cteni are believed to produce micro-turbulence as the fish moves through the water (Fish 1998). One of the most important factors in determining hydrodynamic drag is the boundary layer flow surrounding a fish, due to its effects on friction drag and flow separation (Sagong et al. 2013). Scales, spiny projections, and rough surfaces protruding from the dermis of the fish may act as to stabilize the boundary layer (Webb 1975; Bushnell and Moore 1991), helping to reduce hydrodynamic drag during swimming by generating

vortices around the bodies of the fish to influence flow (Bone 1972; Fish 1998). Although the highly modified cycloid scales of istiophorids lack cteni, it is possible that the spines on these denticular plates on the outermost layer of the dermis serve a similar hydrodynamic function.

Sailfish (*Istiophorus platypterus*) are among the fastest swimming fish in the ocean, reaching burst speeds of 108 km/h (Lane 1941). Juvenile sailfish have been described as having two scale types, which could potentially be similar to those found in the species in the present study: one type is much longer than wide, and was compared to the dermal scutes of the adult, and the second type is circular, with spines which arise from the center (Beebe 1941; Laurs and Nishimoto 1970). Schematic drawings from Nakamura (1985) show scales that are present in sailfish of various body lengths. Two of these images, which are not discussed in the text, depict small ossifications present in scales of young sailfish at body lengths of 15 and 21 cm. These ossifications are circular at the base with spines protruding from the center, and appear very similar to the denticular plates found in the three istiophorid species I observed. Two additional images show the more typical istiophorid scales that are sharply or bluntly pointed, with the anterior ends embedded in the skin of sailfish at body lengths of 90 and 200 cm (Nakamura 1985). Additionally, adult sailfish have been described as having V-shaped protrusions in their skin that point posteriorly (downstream) (Nakamura 1985; Sagong et al. 2008; 2013). These protrusions have been shown to produce pairs of vortices, which create low and high shear stresses at the center and side of the protrusions,

respectively. As these vortices interact with other vortices that are induced from adjacent protrusions, the level of drag is affected. Studies examining this effect have been inconclusive, reporting that drag has decreased in some experimental trials, but not significantly (Sagong et al. 2008). Additionally, experimental design did not allow for testing of hydrodynamic characteristics at maximum swimming speeds, which is most likely when these protrusions would play a role in drag reduction (Sagong et al. 2013).

Further support for a hydrodynamic purpose of the spines on the denticular plates of istiophorids comes from drag-reducing ornaments called riblets, which are found on the dermal denticles of fast-moving sharks. Riblets are small grooves in the denticles that act to passively control flow by limiting the lateral transfer of force, which trains the vortices in the direction of flow (Dean and Bhushan 2010; García-Mayoral and Jiménez 2011; Fletcher 2014). Overall skin friction is reduced by vortices that form and lift away from the denticle wall by the riblets, reducing surface shear stress and loss of momentum (Sagong et al. 2008; Fletcher et al. 2014). Riblets have also been seen in many fossilized Paleozoic fishes, in which they likely served a similar hydrodynamic role (Fletcher 2014).

A significant difference was found between species for scale width and length-to-width aspect ratio. Roundscale spearfish scales were significantly wider than white marlin scales (Figures 8 and 9). Results from the ANCOVA, which suggest that lower jaw fork length does not significantly affect scale length, was expected from my data set, but may not hold for a larger data set. All sampled fish were

adults, and fell within a relatively narrow range for length (171.45–181.61 cm) as well as weight. This is due, in part, to federal regulations that mandate a minimum lower jaw fork length of 66" (167.64 cm) for white marlin and roundscale spearfish, and partially due to the tendency of tournament fish to be the largest specimens caught.

CONCLUSIONS AND FUTURE WORK

Although there is some overlap in general morphological forms depending on the region of the fish from which scales are taken, roundscale spearfish and white marlin scales exhibit considerable inter- and intraspecific morphological variation and differ dramatically between the two species. Scale morphology has been used for distinguishing between these morphologically similar species, and when sampled from specific regions, is a valid character for this purpose. Although the morphology of a single scale is unlikely to be useful for identification, a quick glance at the lateral side of the mid-body is a reasonable and reliable way to confirm the identity of a roundscale spearfish or white marlin, especially in conjunction with the use of a second identifying character such as distance between the vent and anal fin or the length of the branchiostegal rays.

My study presents a fairly comprehensive overview of the scale morphology present in roundscale spearfish and white marlin, but more work is needed. In order to accurately represent the diverse morphological variation present in these species, it would be beneficial to examine even more regions in both species, as well as to extend this sampling strategy to other istiophorids, which may provide the basis to explore the intraspecific variation across istiophorids.

Further, it could potentially be informative to compare the scales of istiophorids to other scombriforms, as well as to other highly migratory, pelagic

species of teleosts to determine if scale morphology could provide an informative character for phylogenetic systematics. Another goal would be to resolve the functional role of the highly modified scales, as well as the denticular plates, and to determine if related species or species that are similar in life history and ecology may have evolved similar structures to fill this functional role, particularly if these adaptations are involved in the facilitation of high performance locomotion. Finally, although challenging to collect specimens at different stages of their life history, sampling marlin and spearfish throughout their ontogeny would be useful in order to examine the development of the adult scales, and to determine at what age (size) the scales transition to their terminal condition. It is possible that scales undergo dramatic changes throughout ontogeny, as juvenile swordfish have scales with small spines present, but transition to adults with scales deeply embedded in the dermis.

CHAPTER 3
TABLES AND FIGURES

Table 1: White marlin scale length (mm), width (mm), and length-to-width aspect ratio for each sampling region including mean and standard deviation, as well as the overall level of variation in scale morphology within the region.

Region	Mean scale length	Std. dev. scale length	Mean scale width	Std. dev. scale width	Mean scale length/width aspect ratio	Std. dev. scale aspect ratio	Level of morphological variation
1	18.67	5.96	1.61	0.27	11.92	4.21	low
2	18.65	3.56	3.39	1.11	5.84	1.32	moderate
3	18.80	2.21	2.05	0.43	9.39	1.46	low
4	19.10	1.67	1.38	0.15	13.96	1.48	low
5	14.52	1.94	1.57	0.25	9.38	1.48	low
6	15.32	1.58	1.78	0.28	8.85	1.85	low
7	22.25	4.73	1.31	0.26	17.36	4.46	low
8	12.57	1.41	1.20	0.26	10.94	2.63	low
9	13.63	1.88	1.81	0.34	7.80	1.72	low
10	15.29	2.41	1.26	0.24	12.59	3.40	low
11	12.22	3.82	1.60	0.49	7.90	2.13	low

Table 2: Roundscale spearfish scale length (mm), width (mm), and length-to-width aspect ratio for each sampling region including mean and standard deviation, as well as the overall level of variation in scale morphology within the region.

Region	Mean scale length	Std. dev. scale length	Mean scale width	Std. dev. scale width	Mean scale length/width aspect ratio	Std. dev. scale aspect ratio	Level of morphological variation
1	21.97	7.10	1.59	0.27	14.20	4.96	low
2	17.20	3.56	3.74	1.31	4.97	1.56	high
3	16.37	2.01	3.47	1.23	5.05	1.18	moderate
4	14.13	1.47	2.56	0.62	5.90	1.73	high
5	13.54	1.90	2.49	0.50	5.69	1.59	moderate
6	12.34	1.26	3.37	0.62	3.80	0.88	high
7	18.38	3.23	1.79	0.38	10.77	2.96	low
8	11.25	3.18	2.12	0.57	5.96	3.30	moderate
9	10.17	1.40	2.93	0.63	3.64	1.00	moderate
10	13.70	3.15	1.75	0.48	8.61	3.48	moderate
11	9.80	2.35	2.70	0.77	3.92	1.44	moderate

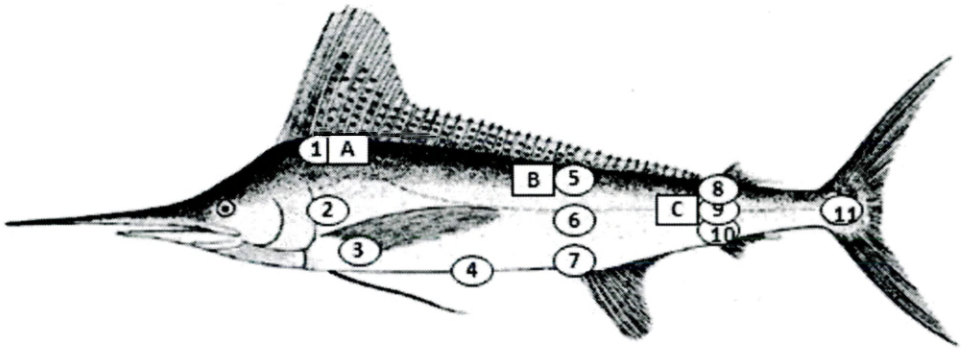


Figure 1: Regions where individual scales were sampled for morphological analyses (1-11) and locations where patches of scales were sampled for clearing and staining (A-C). White marlin drawing from Nakamura (1985).

Figure 2: Cleared and stained scale patches from sampled regions A, B, and C, in white marlin (A1, B1, C1), roundscale spearfish (A2, B2, C2), and blue marlin (A3, B3, C3). All scale bars are 5 mm.

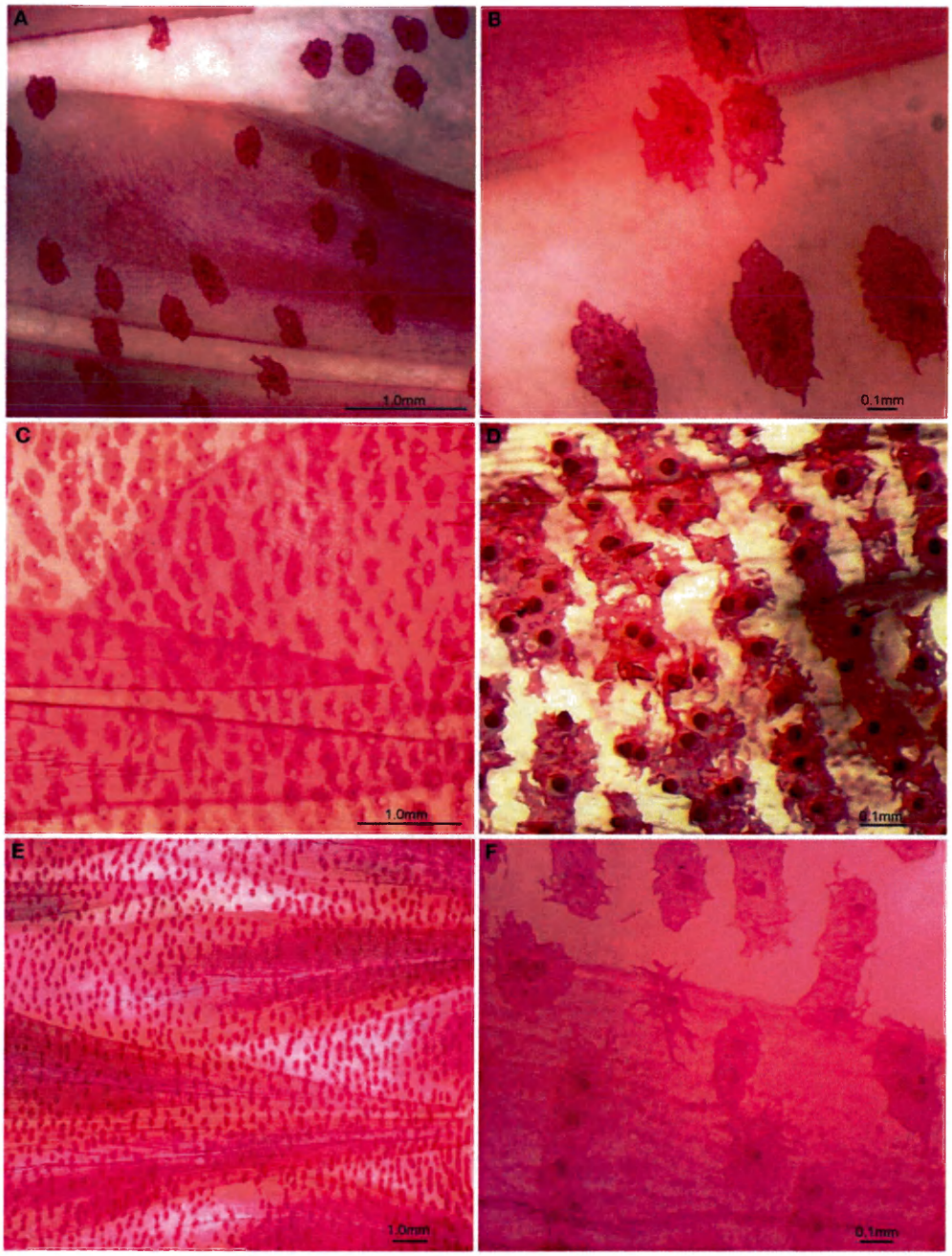


Figure 3: Cleared and stained scale patches showing denticular plates in white marlin (A,B), roundscale spearfish (C,D), and blue marlin (E,F). Scale bars are as labeled.

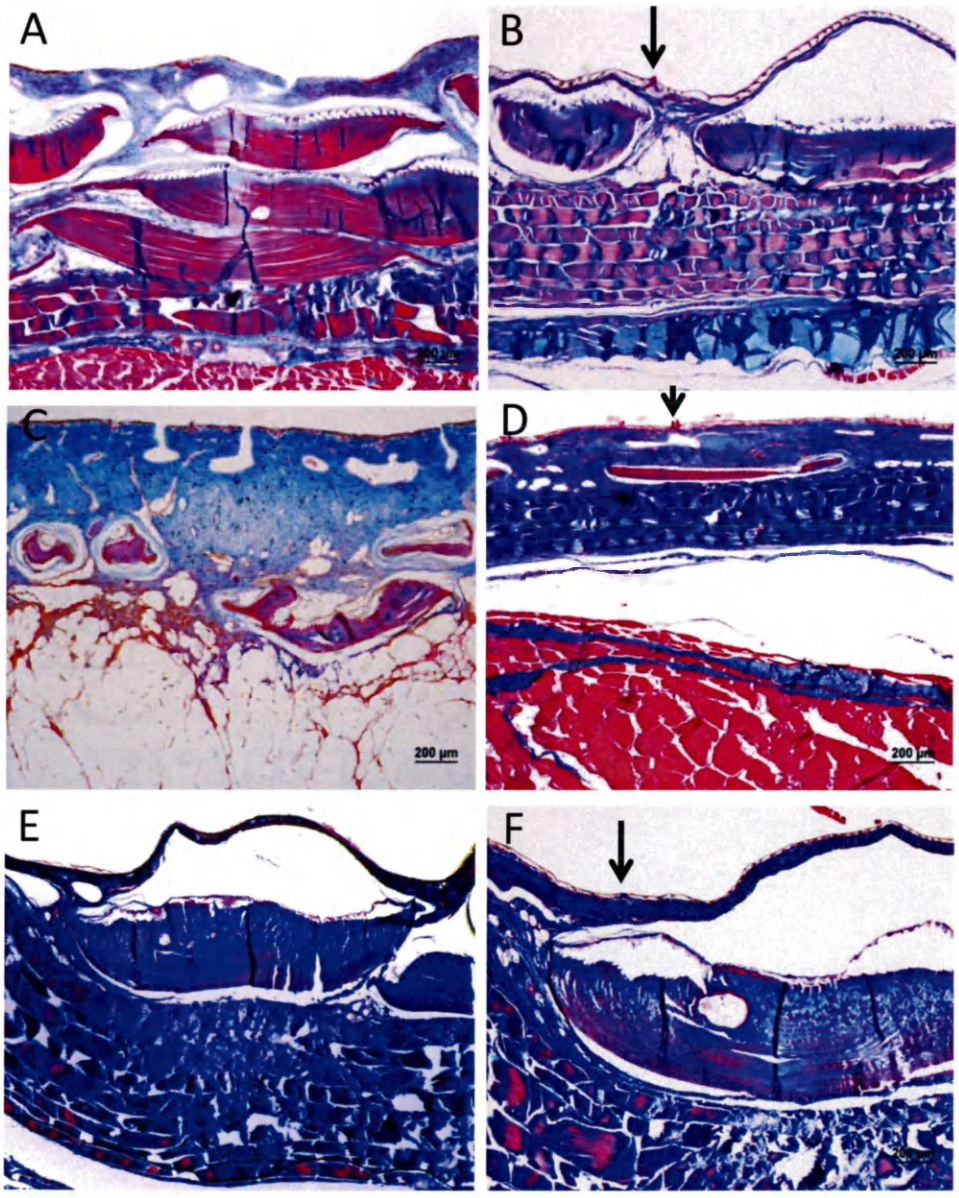


Figure 4: Histological sections show the scales encased in scale pockets, and the denticular plates (indicated by arrows) on a separate layer of the dermis in white marlin (A, B), roundscale spearfish (C, D) and blue marlin (E, F). Also note the heavily imbricated scales of the white marlin compared to the other species.

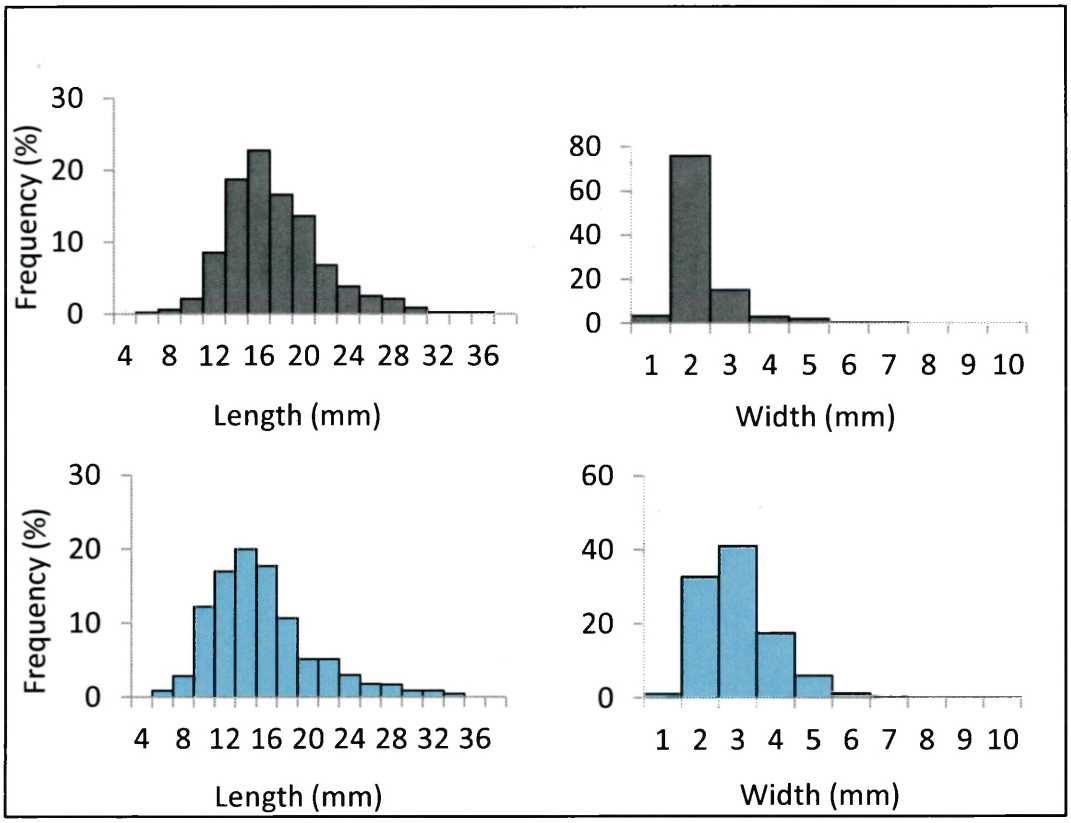


Figure 5: Histograms of scale length (left) and width (right) for white marlin (top) and roundscale spearfish (bottom) for all regions combined.

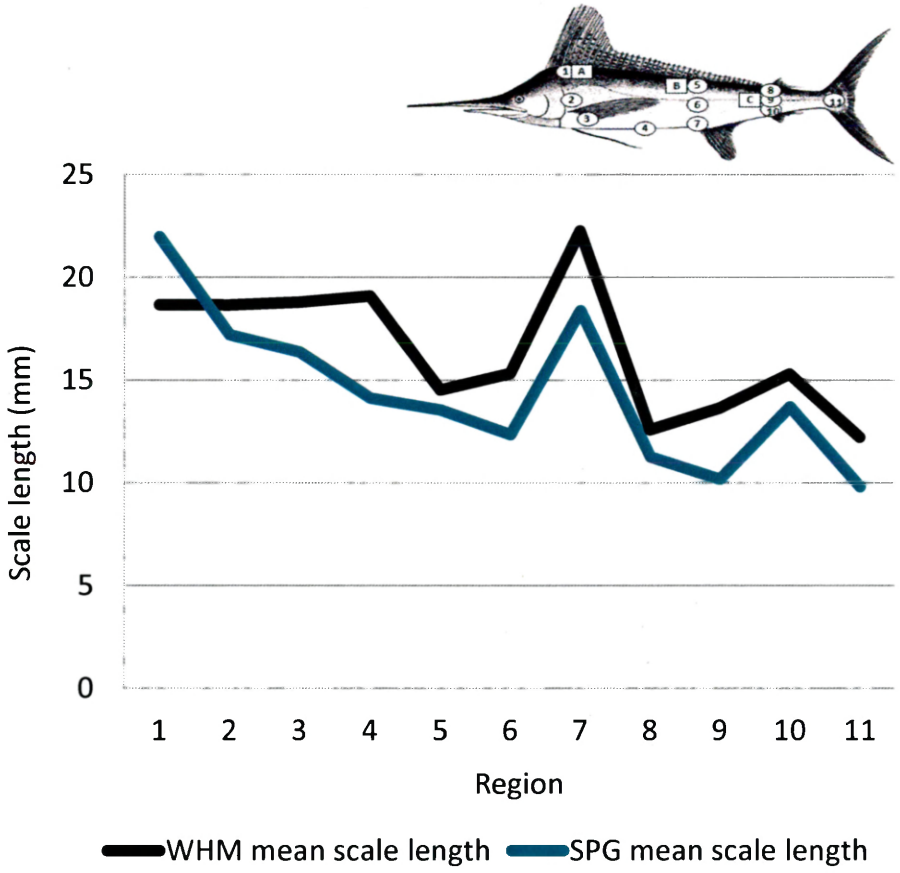


Figure 6: Trends in mean scale length across all regions of white marlin (WHM) and roundscale spearfish (SPG).

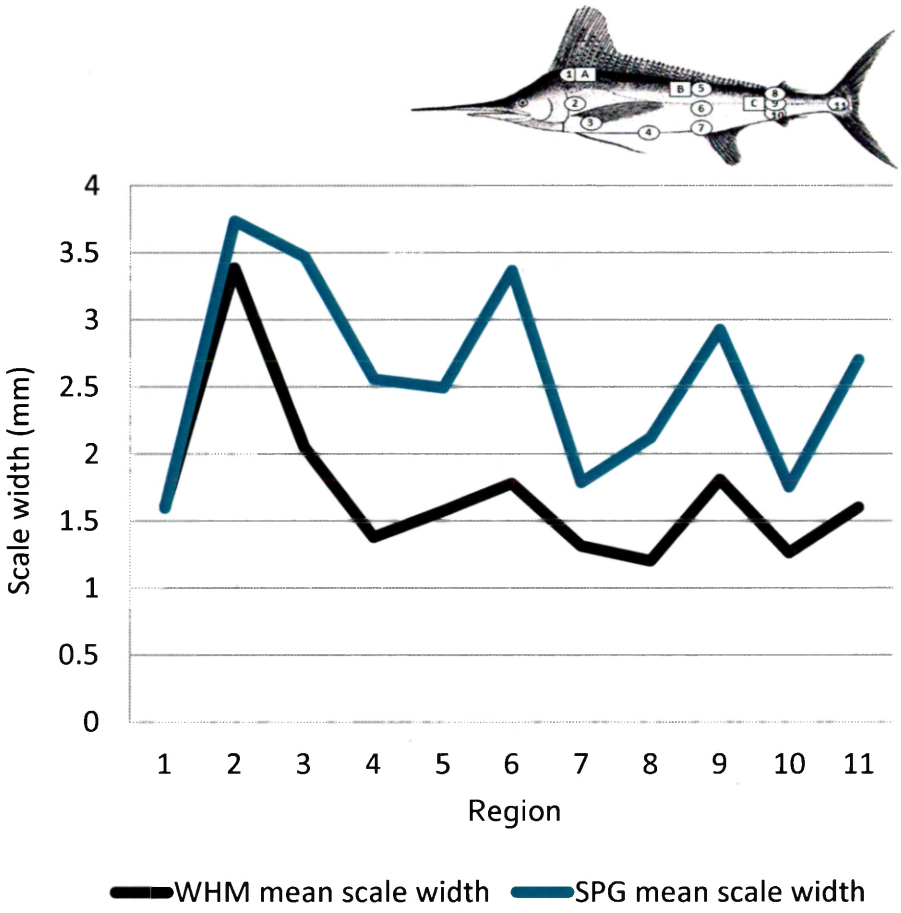


Figure 7: Trends in mean scale width across all regions of white marlin (WHM) and roundscale spearfish (SPG).

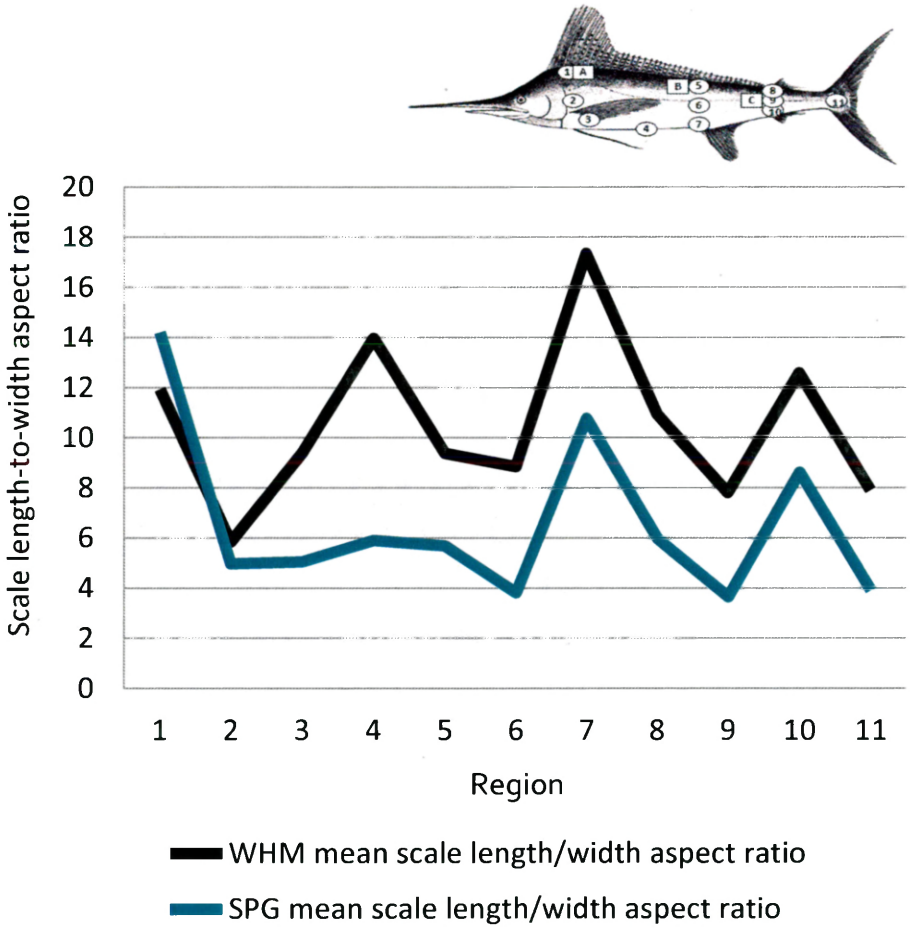
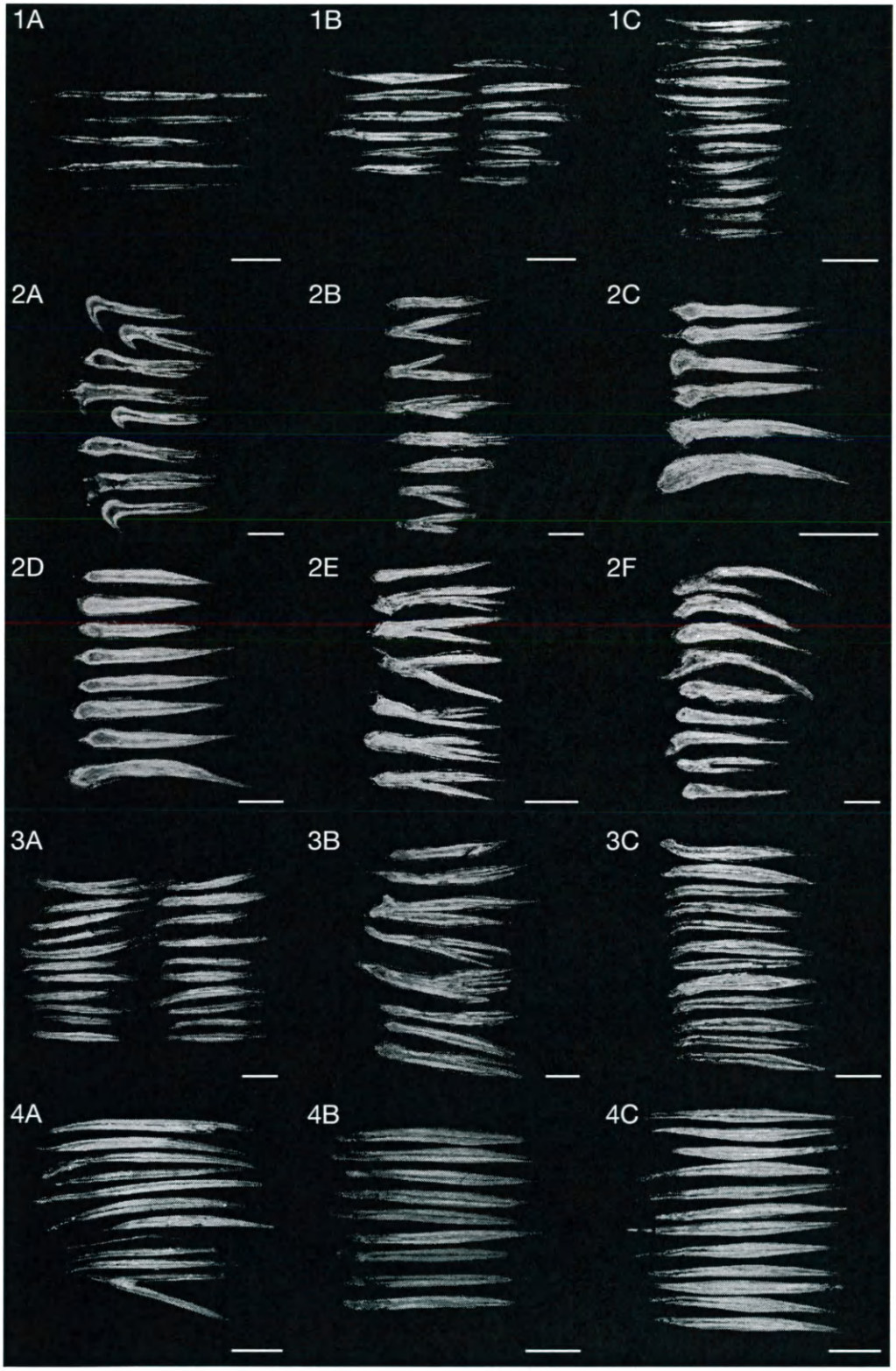
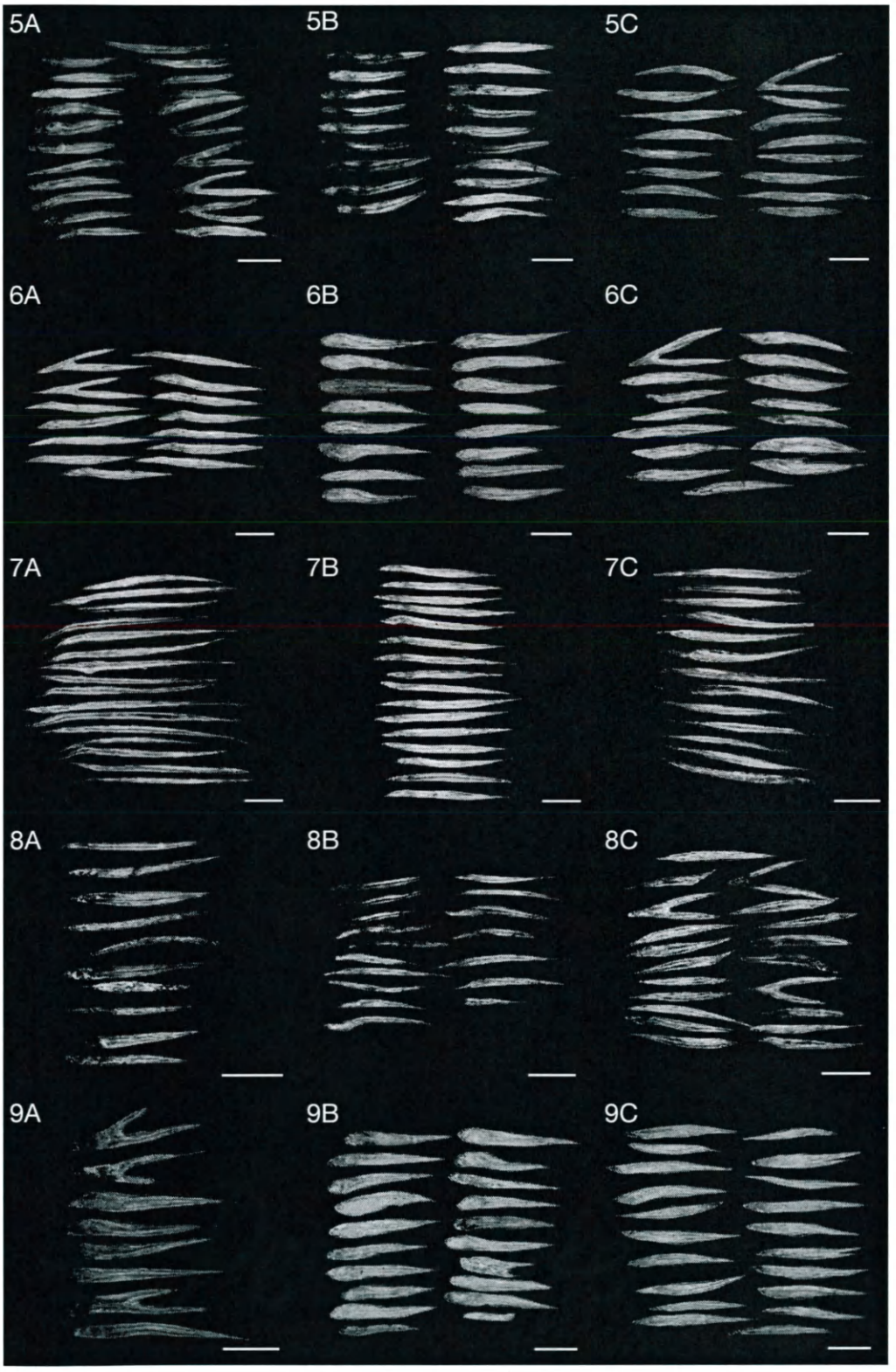


Figure 8: Trends in mean scale length-to-width aspect ratio across all regions of white marlin (WHM) and roundscale spearfish (SPG).

Figure 9: White marlin scales by region. Numbers represent sampling regions as depicted in Figure 1. Letters are used for reference in the text. All scale bars represent 5 mm.


1A
1B
1C
2A
2B
2C
2D
2E
2F
3A
3B
3C
4A
4B
4C


5A
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6A
6B
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7A
7B
7C
8A
8B
8C
9A
9B
9C

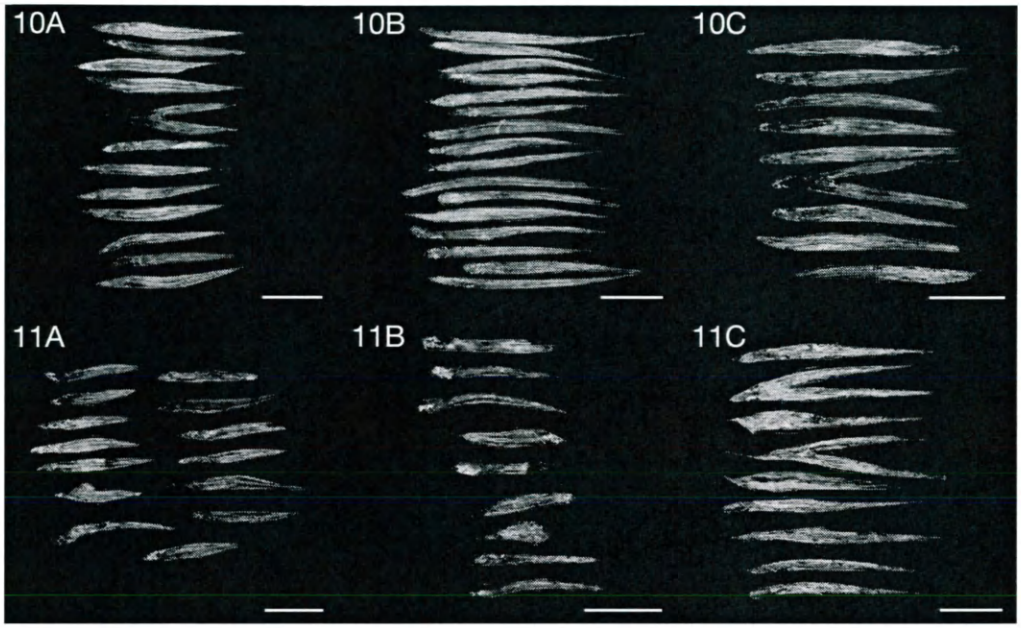
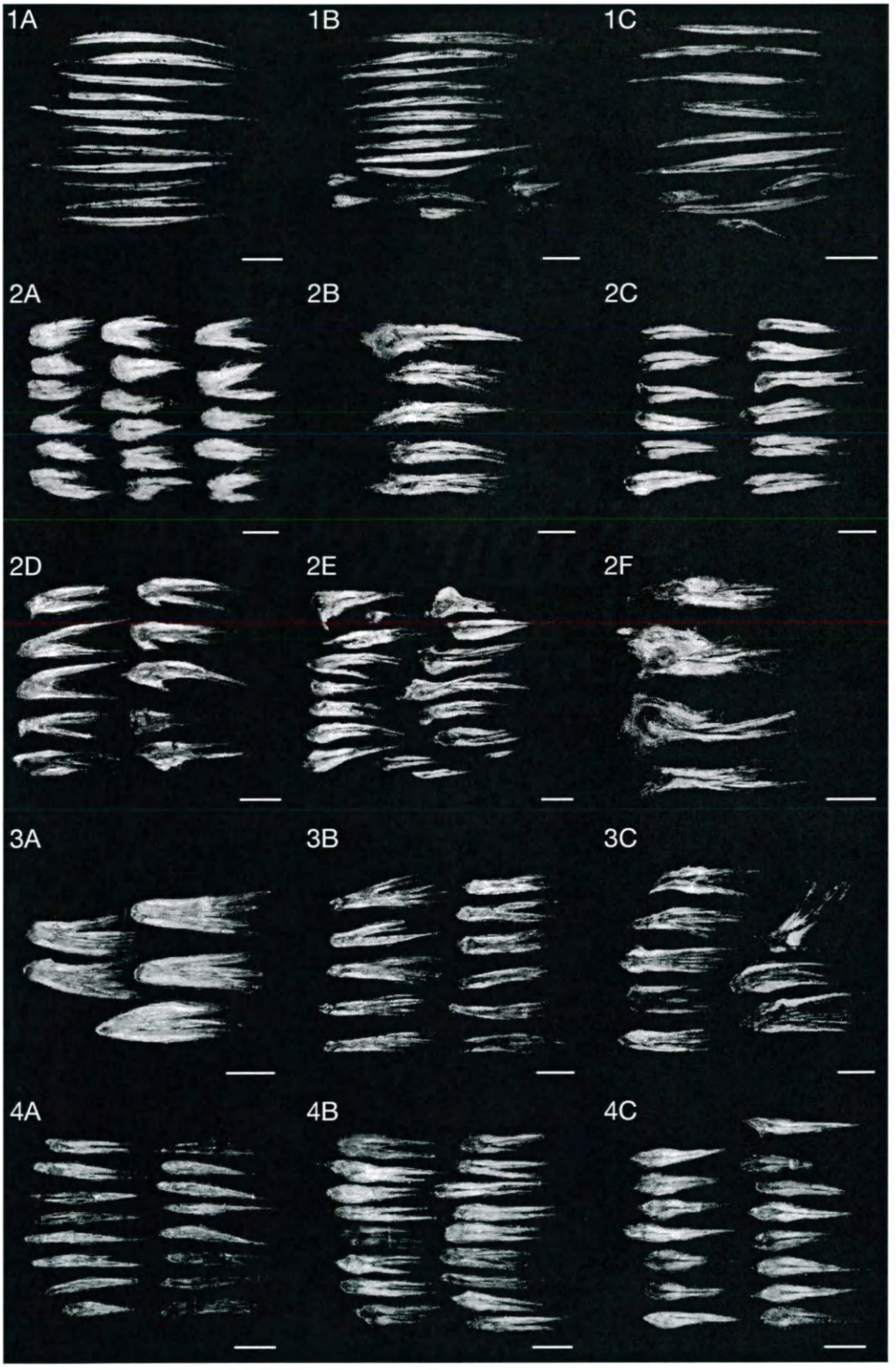

10A
10B
10C
11A
11B
11C

Figure 10: Roundscale spearfish scales by region. Numbers represent sampling regions as depicted in Figure 1. Letters are used for reference in the text. All scale bars represent 5 mm.


1A
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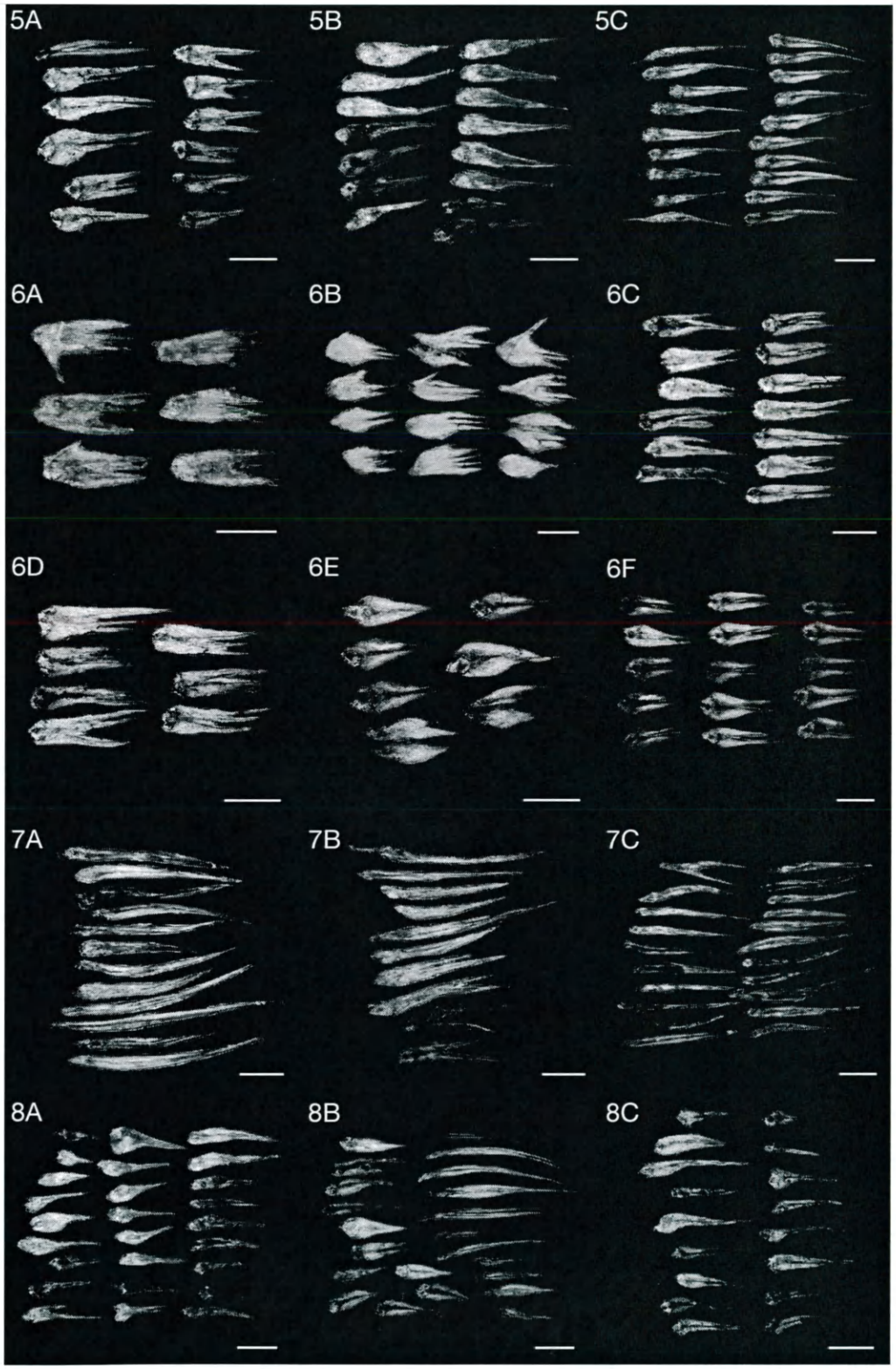
1C
2A
2B
2C
2D
2E
2F
3A
3B
3C
4A
4B
4C


5A
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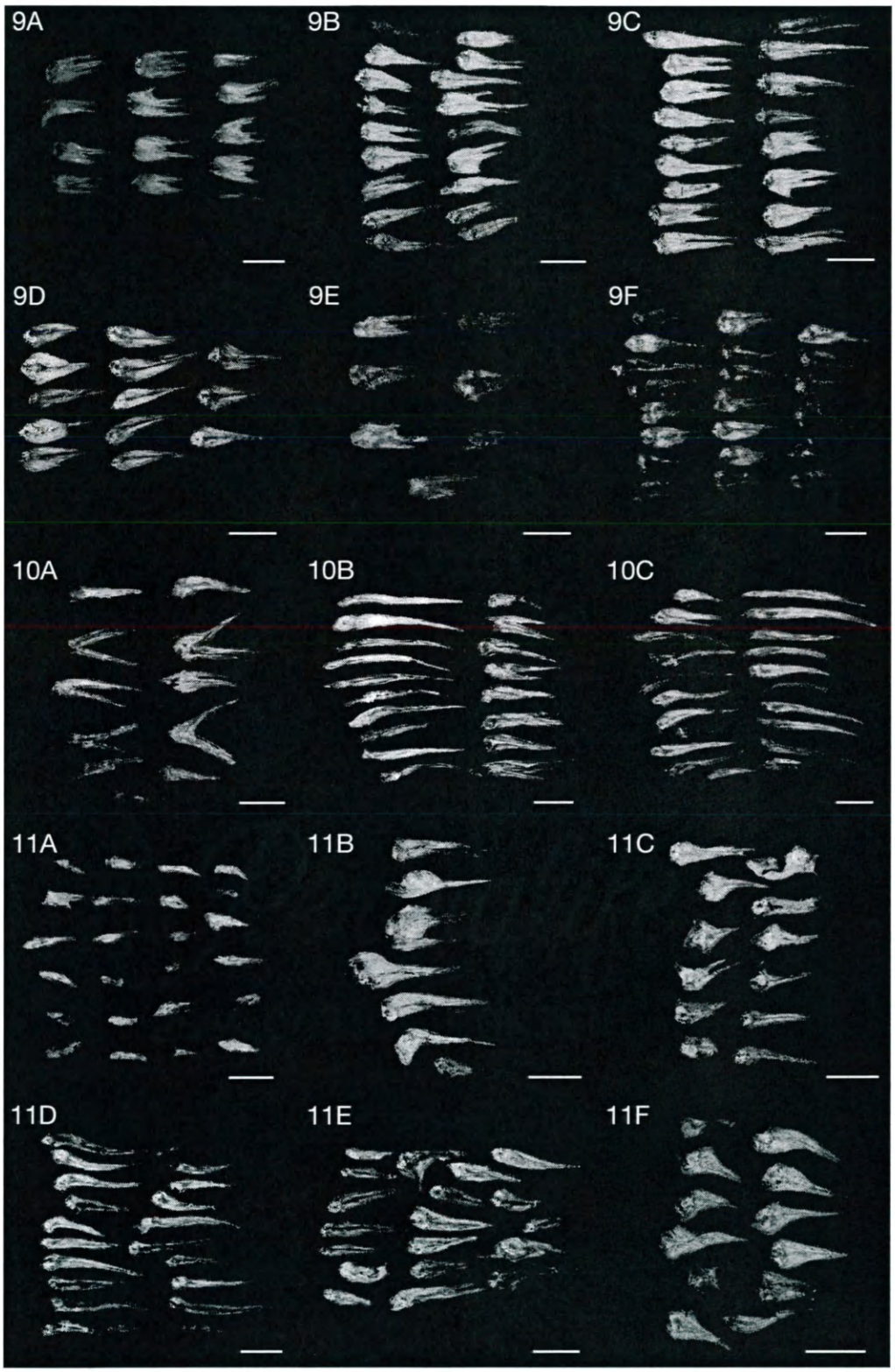
6A
6B
6C
6D
6E
6F
7A
7B
7C
8A
8B
8C


9A
9B
9C
9D
9E
9F
10A
10B
10C
11A
11B
11C
11D
11E
11F

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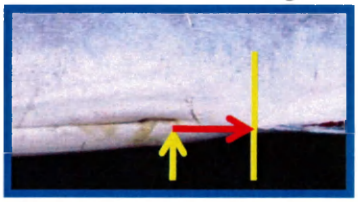
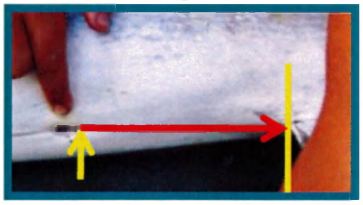
Appendix I

White marlin Roundscale spearfish

Position of vent relative to anal fin

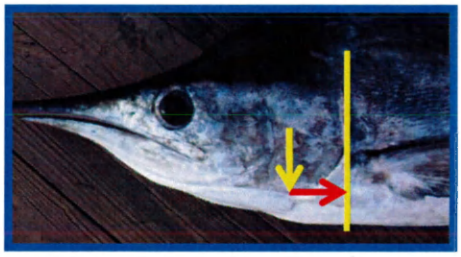


Vent ~2" forward of anal fin

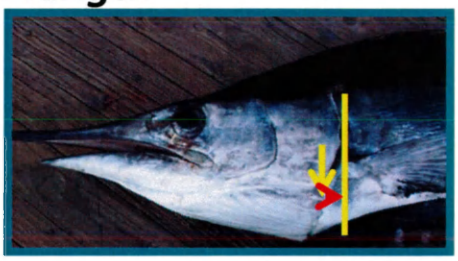


Vent ~6" forward of anal fin

Branchiostegal length



Shorter relative to operculum



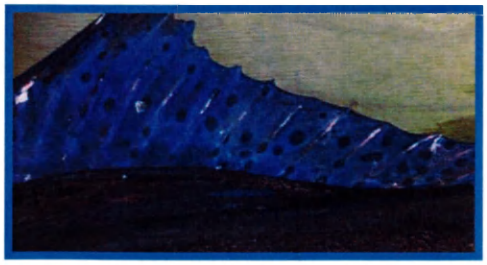
Longer relative to operculum

Scales

Appear pointed at both ends

Appear rounded anteriorly

Dorsal fin spots



Spots on dorsal fin

No spots on dorsal fin

Questions or catches to report?
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VITA

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Born in Reading, PA, on March 1, 1976. Graduated from Schuylkill Valley High School in 1994. Earned a B.S. in Biology from Southampton College of Long Island University in 1998. Worked in fisheries research in Idaho, Maryland, and remote field camps in Alaska. Worked in humanitarian aid and experiential education in Peru and the British Virgin Islands, and taught English as a second language in Costa Rica. Taught traditional sailing and navigation to middle school, high school, and college students while living on six different traditionally-rigged schooners. Worked as a survey technician on the EPA Ocean Survey Vessel *Bold*, and on the NOAA Fisheries Research Vessel *Bell M. Shimada*. Entered the Master's program in Fisheries Science at the Virginia Institute of Marine Science/College of William & Mary in 2010.